New Miocene Horses from the Caliente Formation, Cuyama Valley Badlands, California

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ABSTRACT. Three new equid taxa are recognized from the Caliente Formation: the late Hemingfordian *Parapliohippus* n. gen., the late Clarendonian *Heteropliohippus hulberti* n. gen. and sp., and the late Hemingfordian to late Barstovian *Acritohippus quinni* n. gen. and sp. *Parapliohippus* is known only from the type species, *P. carrizoensis* (Dougherty), which was previously referred to *Merychippus*. *Parapliohippus* is assigned to the tribe Equini and is regarded as the sister taxon of the higher equines (*Pliohippus s.s.*, *Heteropliohippus*, *Astrohippus*, *Onohippidium*, *Hippidion*, *Dinohippus*, and *Equus*). *Heteropliohippus* is assigned to the tribe Equini and is most closely related to *Pliohippus s.s.* and *Astrohippus*. The acritohippines (*Acritohippus tertius*, *A. isonesus*, and *A. quinni*) represent a monophyletic clade whose relationships to the Equini and the Hipparionini are unresolved. The protohippines ("*Merychippus*" *intermontanus*, *Calippus*, and *Protohippus*) represent a monophyletic clade whose relationships to the Hipparionini and the Equini are unclear but are provisionally regarded as the sister group of the Hipparionini.

INTRODUCTION

The Cuyama Badlands, which occur along the eastern side of Cuyama Valley, Ventura County, California (Figure 1), consist of nonmarine strata ranging in age from the Oligocene to the Pleistocene, including the Miocene Caliente Formation. Outcrops of the Caliente Formation also occur north of Cuyama Valley along the northeastern flanks of the Caliente Range and southeast in Lockwood Valley. The Caliente Formation of the Cuyama Valley Badlands has yielded eight mammalian local faunas that range in age from the early Miocene, Hemingfordian North American Land Mammal Age (NALMA), to the late Miocene, Hemphillian NALMA (Gazin, 1930; Wood, 1937; Stock, 1947; James, 1963; J.P. Quinn, 1984; Madden, 1987; Tedford *et al.*, 1987; Kelly and Lander, 1988a, 1988b, 1992; Kelly, 1992). James (1963) described the small mammals that occur in these faunas. However, most of the larger mammals, many representing new taxa, remain undescribed.

Equid fossils from the Cuyama Badlands are relatively abundant. Kelly and Lander (1992) recognized a total of at least 14 equid taxa from the Cuyama Badlands with a maximum diversity of 4 taxa within any local fauna (Table 1). Most of the horse taxa from the Cuyama Badlands are known only from fragmentary specimens consisting of teeth or isolated appendicular elements. However, three of these taxa are now represented by relatively complete cranial material from the Caliente Formation and other Miocene formations of southern California. Reevaluation of the cranial and dental morphology of these three horses indicates that they represent new taxa.

The purpose of this report is to: 1) document the three new Miocene horse taxa from the Caliente Formation and 2) review the phylogenetic relations of these new taxa with those of other late Neogene horse taxa.

METHODS

Measurements of specimens were taken with a vernier caliper to the nearest 0.1 mm. Upper teeth are indicated by uppercase letters and lower teeth by lowercase letters. All teeth were measured along their greatest dimensions. The term "Neogene hypsodont horses" as referred to herein not only includes typical hypsodont horses, such as *Equus* and *Hipparion*, but also includes horses traditionally regarded as mesodont, such as "*Merychippus*" *primus* (Osborn, 1918), and differentiates them from other brachyodont Neogene horses, such as those of the Anchitheriinae. In the discussions of the new genera named herein and in the cladistic analyses, I sometimes compare equid taxa of different hierarchical rank as have other recent investigators of equid phylogeny (Hulbert, 1988a, 1988b, 1989, 1993; Hulbert and MacFadden, 1991). This is often necessary because many of the taxa discussed represent plesions (plesiomorphs) of generic rank (Wiley, 1981); that is, they cannot be assigned to any recognized equid genus without resulting in paraphyly, and the only

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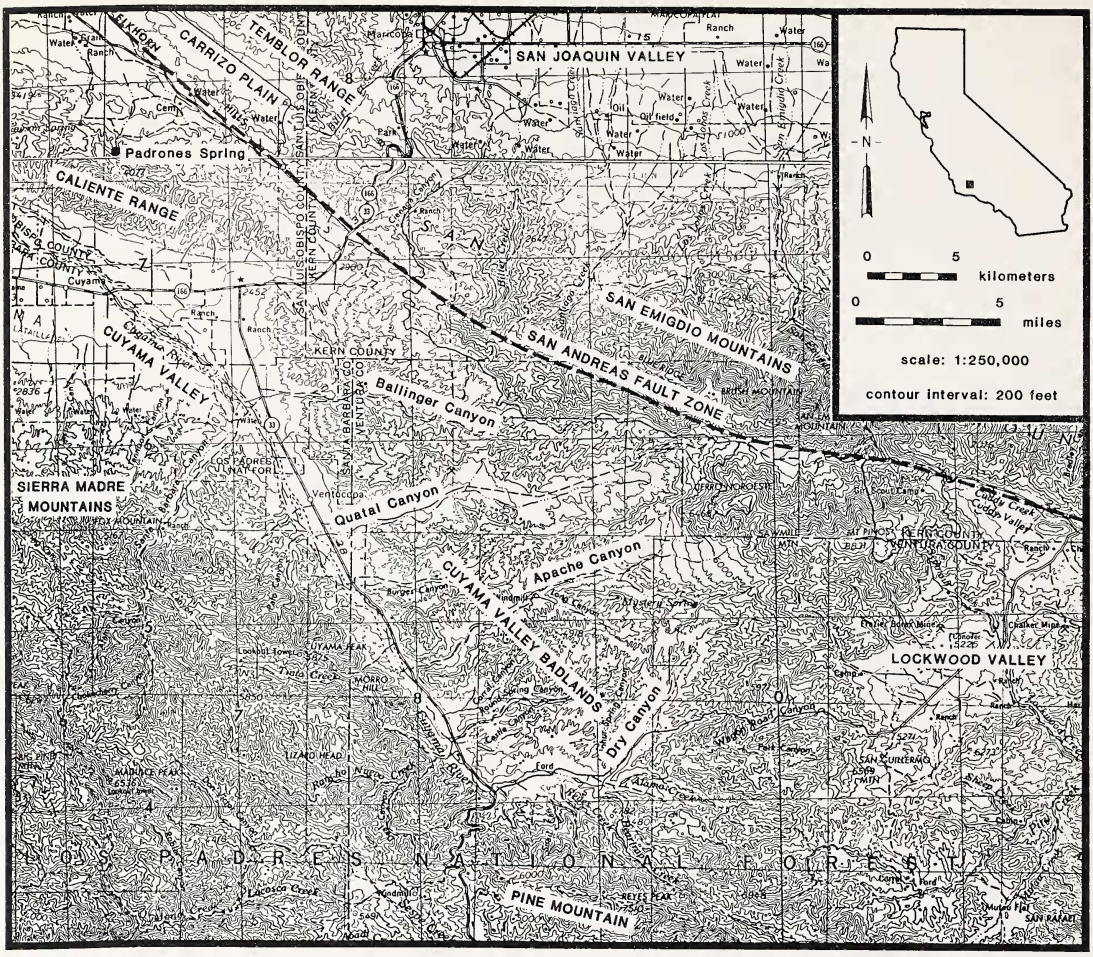

Figure 1. Map showing geographic location of Cuyama Valley Badlands, Ventura County, California. Base maps: U.S. Geological Survey, Cuyama and Taft 1:250,000, 30 × 60 minute quadrangles.

way to refer to them, other than naming a new genus for each one, is to include their specific names (e.g. "*Merychippus*" *stylodontus* [Merriam, 1915], "*Merychippus*" sp. near "*M.*" *sejunctus* [Hulbert and MacFadden, 1991], "*Merychippus*" *goorisi* [MacFadden and Skinner, 1981], "*Dinohippus*" *interpolatus* [Cope, 1893]). Metric abbreviations, dental terminology, and dental formulae follow standard usage.

All cladistic analyses were performed using version 1.5 of the Hennig86 program (Farris, 1988) and run on a 486 personal computer. Cladograms were generated by the IE-BB command. The characters were either equally weighted, the default setting for the Hennig86 program, or successively weighted. Successive character weighting was accomplished by using the XSTEPS W command, which calculates the best fits of each character based on the product of the character consistency and character retention indices. The cladograms produced using successively weighted characters have more steps, but are based on more reliable characters, than those produced using equally weighted characters. The characters and character states used in the cladistic analyses are presented in Appendix A, and the character state matrices for the taxa analyzed are presented in Appendices B and C.

Abbreviations are as follows: APL, greatest anteroposterior length; CV, coefficient of variation; DPOF, dorsal preorbital fossa; L, left; Ma, million years before present; MML, metaconid–metastylid length; N, number of specimens; NALMA, North American Land Mammal Age; OR, observed range; PBL, preorbital bar length; PRL, protocone length; PRW, protocone width; R, right; ROC, radius of curvature; SD, standard deviation; *s.s., sensu stricto;* TR, greatest transverse dimension; UDL, I3–P2 diastema length; UTRL, P2–M3 length.

Institutional acronyms are as follows: AMNH, American Museum of Natural History; F:AM, Frick Collection, American Museum of Natural History; LACM, Natural History Museum of Los Angeles County; LACM(CIT), California Institute of Technology specimen and locality number, specimens now housed at the LACM; UCMP, University of California, Berkeley, Museum of Paleontology; UCR, University of California, Riverside; V-, UCMP vertebrate fossil locality; USNM, United States National Museum.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Order Perissodactyla Owen, 1848

Family Equidae Gray, 1821

Subfamily Equinae Gray, 1821

Tribe Equini Gray, 1821

Parapliohippus new genus

Merychippus, in part, Dougherty, 1940 (pp. 130–133).

Merychippus, in part, Buwalda and Lewis, 1955 (pp. 148–150).

TYPE SPECIES. *P. carrizoensis* (Dougherty, 1940) (previously referred to *Merychippus* and includes *M. carrizoensis* Dougherty and its junior synonym *M. tehachapieneis* Buwalda and Lewis).

REFERRED SPECIES. Known only from the type species, *P. carrizoensis*.

REFERRED SPECIMENS. Skull, AMNH 17061; skull, F:AM 110146; skull, F:AM 110129; partial maxilla with LP2–3, LACM(CIT) 2553; partial maxilla with RP2–4, UCMP 121890; partial maxilla with LP2–M2, UCMP 45114; partial maxilla with RP4–M1 and associated RP2, LACM(CIT) 4919; partial maxilla with LP4–M1, LACM(CIT) 2559; partial maxilla with RP4–M3, LACM(CIT) 4760; partial maxilla with LM1–3, LACM(CIT) 2552; partial maxilla with RM1–3, UCMP 121891; partial maxilla with RP3–M1, LACM 138110; partial maxilla with RdP3, LACM 138100; LP2, LACM 138098; LP2, LACM 138104; RP3, LACM(CIT) 2558; RP3, LACM 138099; RP3, LACM 101152; LP3, UCMP 21972; LP3, UCR 20859; RP4, LACM(CIT) 2560; LP4, LACM 30076; RP4, UCMP 22898; LM1–2, LACM(CIT) 4921; LM1–2, LACM(CIT) 4962; RM1–2, UCMP 82498; LM1–3, LACM(CIT) 4920; RM1, LACM(CIT) 2556; LM1, LACM(CIT) 2564; LM2, LACM(CIT) 4965; RM2, LACM 1350; RM3, LACM 138097; LM3, UCMP 21762; partial dentary with dLp2–4 and Lm1–2, UCMP 82486; partial dentary with Rp2–3, UCR 20856; partial dentary with Rp2–3, UCMP 21688; partial dentary with Lp2–m2, UCMP 21692; partial dentary with Lp2–4, USNM 252734; partial dentary with Rp3–4, USNM 252773; associated dentaries with Lp3–m3 and Rp2–m2, UCMP 11817; partial dentary with Lp3–m1, LACM 138084; partial dentary with Lp3, partial p4, and m1, LACM 138087; partial dentary with Lm1–2, LACM 30114; partial Rp2, LACM 55266; Rp2, LACM(CIT) 2581; Rp3, LACM(CIT) 2573; Rp3, LACM 138091; Rp4, LACM(CIT) 2575; Rm1, LACM(CIT) 2578; Rm2, LACM(CIT) 2576; Rm2, LACM(CIT) 2579; Lm3, LACM(CIT) 2570; partial dentary with Lm3, LACM 138080; Rm3, LACM(CIT) 2574; partial dentary with Rm3, LACM 138085; Lm3, UCMP 21685; Lm3, UCR 14271.

DISTRIBUTION AND AGE. California: Unit 2, Caliente Formation, Caliente Range, late Hemingfordian; Hidden Treasure Spring and West Dry Canyon Local Faunas, Caliente Formation, Cuyama Valley Badlands, late Hemingfordian; Branch Canyon Formation, Santa Barbara Canyon, late Hemingfordian; Phillips Ranch Local Fauna, Bopesta Formation, southern Sierra Nevada, late Hemingfordian; Red Division Local Fauna, Barstow Formation, Mud Hills, late Hemingfordian; Sunrise Canyon Local Fauna, Barstow Formation, Calico Mountains, late Hemingfordian; Yermo Hills Local Fauna, Barstow Formation, Toomey (Yermo) Hills, ? latest Hemingfordian/earliest Barstovian; Barstow Formation, Alvord Mountain, late Hemingfordian; Upper Cady Mountains Local Fauna, Hector Formation, northern Cady Mountains, late Hemingfordian; Daggett Ridge Local Fauna, Barstow Formation, Daggett Ridge, late Hemingfordian; Units 2 and 3, Punchbowl Formation, Cajon Valley, late Hemingfordian; Fernwood Member, Topanga Canyon Formation, Santa Monica Mountains, late Hemingfordian.

Table 1. Equidae of local faunas from the Caliente Formation, Cuyama Badlands, Ventura County, California. NALMA included for each local fauna. Taxonomic assignment follows Kelly and Lander (1992) and this report.

Hidden Treasure Spring Local Fauna (late Hemingfordian)
Parahippus sp. indet.
Parapliohippus carrizoensis (Dougherty, 1940)
Acritohippus sp. cf. *A. tertius* (Osborn, 1918)
West Dry Canyon Local Fauna (latest Hemingfordian)
Parapliohippus carrizoensis (Dougherty, 1940)
Acritohippus quinni n. sp.
Lower Dome Spring Local Fauna (early Barstovian)
Acritohippus quinni n. sp.
Upper Dome Spring Local Fauna (early late Barstovian)
Archeohippus mourningi (Merriam, 1913a)
Acritohippus quinni n. sp.
"*Merychippus*" *brevidontus* (Bode, 1934)
Doe Spring Local Fauna (late Barstovian)
Acritohippus quinni n. sp.
Mathews Ranch Local Fauna (early Clarendonian)
"*Pliohippus*" *tehonensis* (Merriam, 1915)
Heteropliohippus hulberti n. sp.
Hipparion tehonense (Merriam, 1916)
Megahippus sp. indet.
Nettle Spring Local Fauna (late Clarendonian)
Pliohippus or *Protohippus* sp. indet.
Heteropliohippus hulberti n. sp.
Cormohipparion occidentale (Leidy, 1856)
Megahippus sp. cf. *M. matthewi* (Barbour, 1914)
Sequence Canyon Local Fauna (Hemphillian)
"*Dinohippus*" sp. cf. "*D.*" *interpolatus* (Cope, 1893)

DIAGNOSIS. *Parapliohippus* is monotypic; diagnosis for genus is same as for type species. *Parapliohippus* is distinguished from all other genera of the Equinae by having the following suite of characters: 1) frontal bones flat; 2) DPOF with elongated oval shape, deep depth (> 15 mm), anterior margin confluent with face, posterior margin with distinct rim, and posterior pocket present; 3) anterior portion of lacrimal bone reduced and effectively removed from DPOF, except at orbital rim, by extensive posterior development of DPOF; 4) malar fossa anterodorsally directed, relatively deep, slightly pocketed, and well separated posteriorly from DPOF by distinct ridge; 5) relative PBL very narrow (ratio of PBL to UTRL about 0.05); 6) relative muzzle length elongated (ratio of UDL to UTRL about 0.55); 7) cement layer on deciduous premolars very thin and moderately thick on permanent cheek teeth; 8) P3–M2 protocones ovalshaped (ratio of PRL to PRW = 1.2–2.0) and connect with protolophs shortly after onset of wear (about 10% wear); 9) P2–M3 protolophs and metalophs remain separate until greater than 50% worn; 10) upper cheek teeth metastyles common but not well developed; 11) M1–2 protocones connect with hypocones only in late wear; 12) P2 anterostyle large and expanded; 13) P2–M3 with plis caballin absent or rare, external fossette plications rare, if present single and nonpersistent, and internal fossette plications very simple; 14) P2–M2 hypoconal grooves close in moderate wear; 15) P3–4 hypoconal lakes form with closure of hypoconal grooves; 16) P2–M3 strongly curved (ROC < 40 mm); 17) dp1 very reduced, variably present; 18) dp3–4 and p3–m3 protostylids absent or may be present only near base of crowns as anterior cingulids; 19) p2–m3 metaconids and metastylids well separated only in early wear and metaconid–metastylid complexes expanded but not elongated (MML = 45–50% of APL); 20) p2–m3 plis entoflexid commonly present in early wear; 21) p2 ectoflexid moderately deep, partially penetrating isthmus between metaconid and metastylid, and p3–4 ectoflexids deep, completely penetrating isthmuses between metaconids and metastylids; 22) m1–3 metastylids notably smaller and more labially positioned than metaconids; 23) size small (UTRL = 90–100 mm); 24) cheek teeth mesodont (M1 unworn crown height about 25 mm); and 25) feet tridactyl.

ETYMOLOGY. From the Greek *para:* near, beside; in reference to morphological similarities with *Pliohippus.*

DISCUSSION. Dougherty (1940) described *Merychippus carrizoensis* based on the holotype, a partial maxilla with LM1–3 (LACM[CIT] 2552), and a small sample of additional cheek teeth from the Caliente Formation. Buwalda and Lewis (1955) described *Merychippus tehachapiensis* based on the holotype, a partial maxilla with RP4–M1 and associated RP2 (LACM[CIT] 4919), from the Bopesta Formation. Miller (1978) and Munthe (1979) reevaluated the taxonomic relations of these taxa and determined that *M. tehachapiensis* is a junior synonym of *M. carrizoensis.* J.P. Quinn (1984) provided a detailed description of the facial and cheek teeth morphology of this species and determined that it is more closely related to the pliohippines than to *Merychippus s.s.* Other investigators have also recognized that this species is not referable to *Merychippus s.s.* (Woodburne and Tedford, 1982; Woodburne *et al.,* 1982, 1990; Kelly and Lander, 1988b, 1992; Hulbert, 1989, 1993; Hulbert and MacFadden, 1991; Skinner *vide* Macdonald *et al.,* 1992). The cladistic analyses presented below and those of Hulbert (1989) and Hulbert and MacFadden (1991) consistently support recognizing this taxon as a generically distinct clade of the tribe Equini. Furthermore, referral of this species to *Merychippus s.s.* or any other recognized equid genus would result in paraphyly, and its continued assignment to the waste basket, horizontal taxon "*Merychippus,*" is unwarranted. Therefore, it is assigned to *Parapliohippus* n. gen.

Parapliohippus exhibits similarities in certain facial and dental morphologies with *Pliohippus s.s.* and *Astrohippus* but can easily be distinguished from them. *Parapliohippus* differs from *Pliohippus s.s.* by having the DPOF extensively developed, resulting in the effective removal of the lacrimal bone from the fossa. In *Pliohippus s.s.* the lacrimal bone is not reduced anteriorly and extends well into the DPOF. Additional characters exhibited by *Parapliohippus* that distinguish it from *Pliohippus s.s.* are as follows: 1) the relative PBL is narrower; 2) the infraorbital foramen is positioned more anteriorly on the face; 3) the cheek teeth have much thinner cement and are much less hypsodont; 4) the protolophs and metalophs remain separated longer, uniting when the teeth are more than 50% worn; 5) the p3–4 ectoflexids are deeper, completely penetrating the isthmuses between the metaconids and the metastylids; 6) the lateral digits are not reduced; and 7) the size is much smaller.

The facial morphology of *Parapliohippus* differs from that of *Astrohippus* by having a DPOF and malar fossa that are pocketed posteriorly, deeper, and separated from each other by a distinct ridge of bone. *Astrohippus* also possesses a faint dorsoventral ridge that divides the DPOF and malar fossae into anterior and posterior portions, which is lacking in *Parapliohippus.* Additional characters exhibited by *Parapliohippus* that distinguish it from *Astrohippus* are as follows: 1) the relative muzzle length is more elongated; 2) the upper cheek teeth have more curvature and thinner cement and are much less hypsodont; 3) the protocones are less elongated, more oval in shape; 4) the hypoconal grooves close at a later wear stage and lakes are formed on the P3–4 with closure of the grooves; 5) the p2–4 ectoflexids are deeper, penetrating the isthmuses between the metaconids and metastylids; 6) the m1–3 metastylids are smaller and more labially positioned than the metaconids; and 7) the size is much smaller.

Heteropliohippus new genus

TYPE SPECIES. *H. hulberti* n. sp.

DISTRIBUTION AND AGE. Nettle Spring and Mathews Ranch Local Faunas, Caliente Formation, Cuyama Valley Badlands, California, Clarendonian.

REFERRED SPECIES. Only known from type species.

DIAGNOSIS. *Heteropliohippus* is distinguished from all other late Neogene hypsodont horses by having the following suite of characters: 1) frontal bones flat; 2) DPOF shape elongated oval, anterior margin with distinct rim, posterior margin with pronounced rim, and lacking a posterior pocket; 3) malar fossa small, shallow in depth, anteroventrally oriented, and well separated from DPOF; 4) relative PBL narrow (ratio of PBL to UTRL about 0.08); 5) infraorbital foramen positioned posteriorly, about over M1; 6) cement layer moderately thick on deciduous premolars and permanent cheek teeth; 7) P3–M2 protocone occlusal outlines round (ratio of PRL to PRW < 1.2) and protocones connect with protolophs in very early wear; 8) upper cheek teeth metastyles common but not well developed; 9) P2–M3 external fossette plications rarely present, if present nonpersistent, and internal fossette plications very simple; 10) P2–M2 hypoconal grooves close in early wear; 11) P3–M2 hypoconal lakes do not form with closure of hypoconal grooves; 12) P2–M3 moderately curved (ROC about 50 mm); 13) dp3–4 and p3–m3 protostylids moderately well developed; 14) p2–m3 metaconids and metastylids well separated only in early wear and p3–m3 metaconid–metastylid complexes expanded but not elongated (MML = 45–50% of APL); 15) p2–m3 ectoflexids moderately deep, only partially penetrating isthmuses between metaconids and metastylids; 16) p3–4 metastylids and metaconids equal or subequal in size and m1–3 metastylids and metaconids equal or subequal in size and position of their lingual borders; 17) size moderately large (UTRL = 147 mm); and 18) metacarpal V articulates primarily with unciform carpal.

ETYMOLOGY. *Heteros,* Greek for other or different; in reference to proposed relations with pliohippine horses.

DISCUSSION. The recent discovery of two skulls from the middle beds of the Caliente Formation exposed in the Nettle Spring Canyon area, one from an immature individual and one from an adult with associated dentaries and partial foreleg, allows reevaluation of the taxonomic assignment of these specimens. Kelly and Lander (1992) tentatively assigned the two skulls to "*Dinohippus*" n. sp. because they exhibit upper cheek teeth with simple occlusal patterns and a small shallow malar fossa that is well separated from the DPOF, somewhat similar to those of "*Dinohippus*" *interpolatus.* However, further study of these specimens and the cladistic analyses presented below indicate that they represent a distinct clade more closely related to the pliohippines (*Pliohippus* and *Astrohippus*).

Heteropliohippus is derived relative to *Pliohippus s.s.* by having the following character states: 1) the DPOF is unpocketed and bounded anteriorly by a relatively distinct rim and the malar fossa is small, shallow, and unpocketed; 2) the relative PBL is narrow (ratio of PBL to UTRL about 0.08); 3) the infraorbital foramen is positioned posteriorly, about below M1; 4) the upper cheek teeth are moderately curved; 5) the protostylids are moderately well developed; and 6) the metaconids and metastylids are about equal in size and position. Additional characters exhibited by *Heteropliohippus* that distinguish it from *Pliohippus s.s.* are as follows: 1) the cement on the cheek teeth is thinner; 2) the P3–M2 protocones connect with the protolophs at a later wear stage; and 3) P3–M2 hypoconal lakes do not form with closure of the hypoconal grooves. The above distribution of character states and the cladistic analysis presented below indicate that *Heteropliohippus* is not referable to *Pliohippus s.s.*

Heteropliohippus differs from *Astrohippus* by having the following characters: 1) the posterior margin of DPOF with a pronounced rim; 2) the malar fossa is small, shallow, and well separated from the DPOF; 3) the cement layer on the permanent cheek teeth is thinner; 4) the protocones are oval-shaped; 5) the P3–M2 protocones connect with the protolophs in very early wear; 6) the M1–3 plis caballin are common, but small and nonpersistent; 7) the p3–m3 protostylids are well developed; and 8) the p2–4 ectoflexids are moderately deep and partially penetrate the isthmuses between the metaconids and metastylids. Evander (1993) recently hypothesized that *Astrohippus* may possess the autapomorphic character state of abbreviated metapodials and slender, elongated phalanges. Evander's hypothesis was based on his analysis of faunas containing *Astrohippus* and not supported by definitive evidence. However, if proven true with further study, then this autapomorphy would further differentiate *Heteropliohippus* from *Astrohippus.*

Heteropliohippus differs from *Dinohippus* by having the following characters: 1) the DPOF is relatively deep and has a distinct rim at the anterior margin; 2) the relative PBL is narrow (ratio of PBL to UTRL = 0.08); 3) the cement layer on deciduous premolars and the permanent cheek teeth is moderately thick; 4) the P3–M2 protocones connect with the protocones at an earlier wear stage; 5) upper cheek teeth internal fossette plications are very simple; 6) the P2–M2 hypoconal grooves close in early wear; 7) the dp3–4 and p3–m3 protostylids are moderately well developed; 8) the p2–4 ectoflexids are moderately deep and partially penetrate the isthmuses between the metaconids and metastylids; 9) the m1–3 metastylids and metaconids are equal or subequal in size and position of their lingual borders; and 10) the size is moderate (UTRL = 147 mm).

It is well recognized that many equid dental characters exhibit a moderate degree of intraspecific and

ontogenetic variation (MacFadden, 1984a). At higher taxonomic levels, such as generic or tribal, equid dental characters are also prone to homoplasy and reversal (Hulbert, 1989; Hulbert and MacFadden, 1991). However, in studies where large equid samples were available, certain facial and dental morphologies were found to be conservative; that is, they exhibited low degrees of intraspecific or intrageneric variation. For example, MacFadden (1984a) performed a comprehensive statistical analysis on a large quarry sample of *Hipparion tehonense* (Merriam, 1916) to determine the amount of individual, sexual, and ontogenetic variation within the sample. He also studied pooled samples of other equid genera and species. MacFadden's (1984a) study resulted in the following conclusions: 1) facial fossae morphology is not significantly influenced by individual variation, sexual dimorphism, or ontogeny, and facial fossae are taxonomically valid character complexes for generic determination; 2) qualitative characters of the upper cheek teeth are not affected significantly by sexual dimorphism, but many are significantly affected by ontogeny; and 3) most measured characters of the upper cheek teeth are taxonomically valid. The taxonomic significance of facial fossae morphology has also been well documented by other investigators (e.g. Woodburne, 1982, 1989; J.P. Quinn, 1984; Hulbert, 1988a, 1988b, 1989; Kelly and Lander, 1988b; Hulbert and MacFadden, 1991). Although MacFadden (1984a) demonstrated that many qualitative characters of the upper cheek teeth are prone to ontogenetic variation, Hulbert (1988a, 1988b, 1989) and Hulbert and MacFadden (1991) have shown that, after ontogenetic variation has been accounted for, equid genera can be distinguished by a suite of qualitative dental characters. Because the sample size of *Heteropliohippus* is small, the amount of ontogenetic variation for many of its cheek teeth characters remain undetermined. However, certain qualitative cheek teeth character states of *Heteropliohippus* can be confidently compared with those of other equid genera. For example, in *Pliohippus s.s., Dinohippus,* and *Parapliohippus,* after initial wear, the m1–3 metastylids are consistently smaller and more labially positioned than the metaconids, whereas in the sample of *Heteropliohippus,* which includes moderately worn lower molars, the metastylids are about equal in size and position. In *Astrohippus,* the p2–4 ectoflexids are shallow and do not penetrate the isthmuses between the metaconids and metastylids regardless of the amount of wear, whereas in the sample of *Heteropliohippus,* which includes moderately worn lower premolars, the ectoflexids partially penetrate the isthmuses. Certain other qualitative cheek teeth characters are either absent or present in a genus and, thus, are not affected by ontogeny. For example, in *Pliohippus s.s., Astrohippus, Dinohippus,* and *Parapliohippus,* protostylids are absent or may be very weakly developed as small anterior cingulids near the base of the crowns, whereas in *Heteropliohippus,* moderately well-developed protostylids are present that extend well up from the base of the crowns. In *Pliohippus s.s., Dinohippus,* and *Astrohippus,* the cement on the upper cheek teeth is significantly thicker than that of *Heteropliohippus.* Even if some of the qualitative cheek teeth characters listed in the diagnosis of *Heteropliohippus* have to be modified when a larger sample is available, its distinctive facial morphology, a character complex that has been shown to be taxonomically significant and not strongly influenced by ontogeny, sexual dimorphism, or individual variation in other equid genera, and the qualitative dental characters noted above still support recognizing *Heteropliohippus* as generically distinct from all other Neogene hypsodont horses. This conclusion is further supported by the cladistic analyses presented below, which indicate that *Heteropliohippus* represents a generically distinct clade that together with *Pliohippus s.s.* and *Astrohippus* form a monophyletic lineage, wherein *Pliohippus s.s.* is the closest sister taxon to *Heteropliohippus,* and *Heteropliohippus* is the closest sister taxon to *Astrohippus.*

Heteropliohippus hulberti
new species

Figure 2, Tables 2–3

"*Dinohippus*" n. sp. Kelly and Lander, 1992 (p. 4, appendix 1).

HOLOTYPE. Associated partial skull with RP2–M3 and partial LdP1, P2–4, M2–3, partial dentaries with Rp2–m3 and Lp2–m3, partial distal radius, carpals, partial proximal metapodials, first medial phalanx, and second medial phalanx, LACM 133452.

TYPE LOCALITY. LACM 6106.

DIAGNOSIS. Same as for genus.

ETYMOLOGY. Named in honor of Richard C. Hulbert, Jr., of the Georgia Southern University in recognition of his many contributions to our understanding of the phylogeny of Neogene horses.

REFERRED SPECIMENS. Partial immature skull with right and left dP1–4, LACM 134494; partial upper left cheek tooth, LACM 136055; partial upper left cheek tooth, LACM 136056; associated LdP3–4 and Rdp2, LACM 136054.

DISTRIBUTION AND AGE. Same as for genus.

DESCRIPTION. In the holotype partial skull of *Heteropliohippus hulberti,* the left facial region is preserved from the preorbital bar anteriorly to just above the P2 and the right facial region from the posterior aspect of the DPOF anteriorly to just above the dP1 (Figure 2A). Although the posterior portion of the referred immature skull is badly fractured, the right and left facial regions are well preserved. MacFadden (1984a) demonstrated that facial fossa morphology is not significantly affected by ontogeny; thus, the immature skull can be confidently assigned to *H. hulberti* because its facial fossae

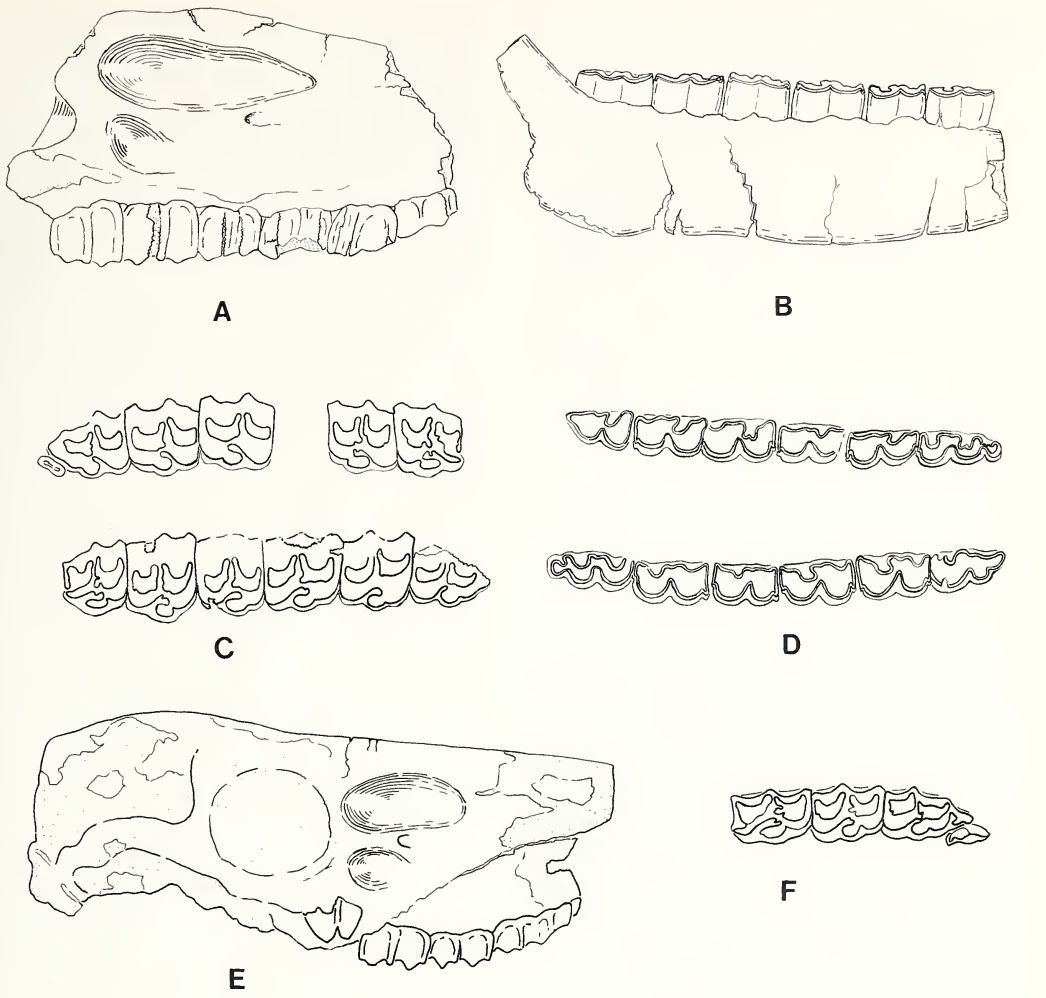

Figure 2. *Heteropliohippus hulberti* n. gen. and sp. **A–D,** Holotype, LACM 133452: **A,** partial skull, right lateral view; **B,** partial right dentary, lateral view; **C,** RP2–M3 and partial LdP1, P2–4, M2–3, occlusal view; **D,** Rp2–m3 and Lp2–m3, occlusal view. **E,** Immature skull, LACM 134494, right lateral view. **F,** RdP1–4, LACM 134494, occlusal view. Scale = 10 mm.

morphology closely matches that of the holotype. The facial morphology is characterized by a moderately deep DPOF that is well separated from a small distinct malar fossa. The preorbital bar is partially damaged in the holotype but appears to have been narrow in width, as is the condition in the referred skull (Figure 2E).

The DPOF (Figures 2A, 2E) is characterized by having the following: 1) the dorsal and posterior margins are formed by a continuous, distinct, rounded rim; 2) the anterior margin is formed by a low distinct, rounded rim; 3) the ventral margin is confluent anteriorly with the face, whereas posteriorly it is separated from the malar fossa by a prominent ridge; 4) the depth is moderate (12–14 mm); 5) a pocket is lacking in the posterior aspect; and 6) the shape is an elongated oval.

The malar fossa (Figures 2A, 2E) is characterized by having the following: 1) the dorsal margin is formed by a distinct ridge separating it from the DPOF; 2) the posterior margin is bounded by a low, rounded ridge; 3) the anterior margin is anteroventrally oriented and confluent with the facial crest; 4) the depth is shallow (5–6 mm); 5) a pocket is lacking in the posterior aspect; and 6) the shape is oval (APL = 19 mm, TR = 17 mm).

The deciduous P1 (Figure 2F) is relatively large in the immature skull and likewise in the adult as indicated by the broken crown in the holotype. The deciduous P2–4 (Figure 2F) are characterized by the following: 1) the cement layer is moderately thick; 2) the mesostyles are distinct, but not prominent; 3) the external fossette margins are very simple with only a slight indication of plis protoloph;

Table 2. Measurements (in mm) of upper dentition of holotype of *Heteropliohippus hulberti* n. sp. from the Caliente Formation. a = approximate.

Dimension		Right	Left
P2	APL	29.7	29.3
	TR	—	21.9
P3	APL	26.7a	26.8
	TR	—	27.0
P4	APL	—	26.9
	TR	26.0a	26.1
M1	APL	26.5a	—
	TR	23.5a	—
M2	APL	23.8	23.7
	TR	24.0a	23.9
M3	APL	24.3	24.6
	TR	23.6	23.7
P2–4	APL	78.3	78.2a
M1–3	APL	—	69.3
P1–M3	APL	—	153.5a
UTRL		146.3a	146.8

4) the internal fossette margins are very simple with single plis postfossette that have shallow rounded outlines; 5) the occlusal outlines of the dP2–3 protocones are round, whereas the occlusal outline of the dP4 protocone is an elongated oval (probably wear-related); 6) the protocones connect with the protolophs in early wear; 7) the plis caballin are very small indentations; and 8) the hypoconal grooves are shallow and nonpersistent, being completely lost in early wear.

The permanent upper cheek teeth (Figure 2C) are characterized by having the following: 1) the cement layer is moderately thick; 2) the mesostyles are distinct, but not prominent; 3) the internal fossette margins are very simple with the plis postfossette single, weakly developed, and nonpersistent; 4) the external fossette margins are very simple with the plis protoloph absent or weakly expressed as small nonpersistent indentations; 5) the hypoconal grooves are weakly developed and close in early wear; 6) the plis caballin are small and nonpersistent; 7) the protocones connect with the protolophs in early wear; and 8) the occlusal outlines of the protocones are round in the premolars and progressively become slightly elongated from the M1 to the M3 (probably wear-related).

Table 3. Measurements (in mm) of lower dentition of holotype of *Heteropliohippus hulberti* n. sp. from the Caliente Formation. a = approximate.

Dimension		Right	Left
p2	APL	24.0a	23.9
	TR	—	15.8
p3	APL	24.5	24.7
	TR	16.2	16.2
p4	APL	25.0	24.8
	TR	16.1	16.1
m1	APL	22.2	22.6a
	TR	15.3	15.5
m2	APL	25.0a	25.4
	TR	13.9	13.9
m3	APL	28.0a	28.1
	TR	12.5	12.6
p2–4	APL	72.4	74.0a
m1–3	APL	73.7a	72.5
p2–m3	APL	147.4	147.0a

Although the dentary anterior to the Rp2 in the holotype is slightly damaged, there is no alveolus or root to indicate that a dp1 was present. The lower premolars and molars (Figure 2D) are characterized by the following: 1) the cement layer is moderately thick; 2) the metaconids and metastylids are not well separated and the metastylids are equal in size or slightly smaller than the metaconids; 3) the p3–m2 protostylids are moderately well developed; and 4) the ectoflexids are moderately deep and partially penetrate the isthmuses between the metaconids and metastylids.

The partial lower foreleg of the holotype of *Heteropliohippus hulberti* has the carpals and anterior portion of the metacarpals preserved. A distinct articulation facet is present on the unciform carpal for metacarpal V. The partial metacarpals II and IV are well developed, which may indicate that the manus was tridactyl. The associated central first and second phalanges are of normal equid proportions.

The measurements of the teeth of *Heteropliohippus hulberti* are presented in Tables 2 and 3.

DISCUSSION. Merriam (1915) described *Protohippus tehonensis* based on a single, well-worn LM1 (UCMP 21779) from the Santa Margarita Formation, Tejon Hills, California. Merriam (1916) also tentatively referred a lower premolar to this species. Stock (1935) provisionally assigned a partial right dentary with a broken dp2, dp3–4, and m1 (LACM[CIT] 1825) from a well core in the Santa Margarita Formation to this species. Drescher (1941) referred two additional specimens from the Tejon Hills to this species, a Lp2–4 (LACM[CIT] 2617) and a Lm1–3 (LACM[CIT] 2618), but regarded this taxon as belonging to the genus *Pliohippus*. Savage (1955) also assigned this species to *Pliohippus*. Additional material of *Pliohippus tehonensis* from the early Clarendonian Mathews Ranch Local Fauna has been identified by James (1963) and Kelly and Lander (1992). Hulbert (1987a) regarded this taxon as a separate clade from *Pliohippus s.s.* and noted that it exhibits the proper mixture of plesiomorphic and apomorphic character states that could allow it to be the sister taxon of some segment of the *Astrohippus–Equus–Dinohippus* clade. Recently, Hulbert (1993, fig. 1) referred this species to "*Dinohippus*" *tehonensis*. However, the generic status of this species cannot be confidently determined because the facial morphology is unknown (Hulbert, 1987a). For this reason, it is herein referred

to "*Pliohippus*" *tehonensis*. The cheek teeth of *Heteropliohippus hulberti* are morphologically similar to those of "*Pliohippus*" *tehonensis*, but they differ from those of "*Pliohippus*" *tehonensis* by having the following characters: 1) the upper cheek teeth have less distinct hypocones, less persistent hypoconal grooves, and less anteroposterior elongation of the protocones; 2) the lower cheek teeth are relatively wider transversely and have better developed protostylids; and 3) the lower molars have shallower ectolophids and the metastylids and metaconids are equal or subequal in size and position of their lingual borders. The above differences clearly indicate that *Heteropliohippus hulberti* and "*Pliohippus*" *tehonensis* represent different species, but whether they belong to the same genus cannot be determined because the facial morphology of "*Pliohippus*" *tehonensis* is unknown. However, if the facial morphology of "*Pliohippus*" *tehonensis* is determined with future discoveries to be similar to that of *Heteropliohippus hulberti*, then *Heteropliohippus hulberti* and "*Pliohippus*" *tehonensis* could conceivably be derived from a common ancestor and "*Pliohippus*" *tehonensis* would be referable to *Heteropliohippus*.

Drescher (1941) described *Pliohippus leardi* based on the holotype, an isolated LM1 (LACM[CIT] 2645), and a small topotypic sample of upper and lower cheek teeth from the Chanac Formation, Tejon Hills, California. Savage and Russell (1983) and Hulbert (1993) refer to this species as "*Dinohippus*" *leardi*. Hulbert (1993, fig. 1) regarded "*Pliohippus*" *tehonensis* as the closest sister taxon to "*Dinohippus*" *leardi*. Hulbert (1993) also indicated that "*Dinohippus*" *leardi* gave rise to *Astrohippus* by cladogenetic speciation and was also the inferred ancestor that gave rise by cladogenetic speciation to the *Hippidion–Onohippidium* clade and to the "*Dinohippus*" *interpolatus–*"*Dinohippus*" *mexicanus–Equus simplicidens* clade. Like "*Pliohippus*" *tehonensis*, the generic status of "*Dinohippus*" *leardi* cannot be determined confidently because the facial morphology is unknown. *Heteropliohippus hulberti* differs from "*Dinohippus*" *leardi* by having the following characters: 1) the cheek teeth are smaller; 2) the protocones are less anteroposteriorly elongated; 3) the hypoconal grooves are less developed and disappear in an earlier wear stage; and 4) the lower molars have moderately well-developed protostylids and shallower ectolophids, and the metastylids and metaconids are equal or subequal in size and position of their lingual borders.

Tribe Undetermined

Acritohippus new genus

Hippotherium, in part, Cope, 1889 (pp. 451–454).
Merychippus, in part, Osborn, 1918 (pp. 101–102, 105).
Stylonus, in part, Kelly and Lander, 1988b (p. 4), 1992 (p. 3, appendix 1).

TYPE SPECIES. *A. isonesus* (Cope, 1889) (previously referred to *Hippotherium*, *Merychippus*, and *Stylonus*).

DISTRIBUTION AND AGE. California: Caliente Formation, latest Hemingfordian to late Barstovian; Bopesta Formation, late Barstovian; Barstow Formation, latest Hemingfordian. Florida: Torreya Formation, early Barstovian. Oregon: Mascall Formation, early Barstovian; Sucker Creek Formation, late Barstovian. Nebraska: Box Butte Formation, late Hemingfordian; Sheep Creek Formation, late Hemingfordian. Nevada: Virgin Valley Formation, early Barstovian; Highrock Canyon Sequence, early Barstovian. Montana: Six Mile Creek Formation, early Barstovian.

REFERRED SPECIES. *A. tertius* (Osborn, 1918) (previously referred to *Merychippus*); *A. quinni* n. sp.

DIAGNOSIS. *Acritohippus* is distinguished from all other Neogene hypsodont horses by having the following suite of characters: 1) frontal bones flat; 2) facial crest dorsoventrally compressed; 3) DPOF shape oval, depth shallow to deep (5 to > 15 mm), anterior margin confluent with face, ventral margin lacking pronounced rim, posterior margin with distinct rim, and posterior pocket shallow or absent; 4) malar fossa shallow in depth (< 10 mm) and confluent with DPOF; that is, malar fossa and DPOF only separated posteriorly by low, indistinct ridge; 5) relative PBL very narrow (ratio of PBL to UTRL about 0.05); 6) muzzle width relative to UTRL broad (> 36%); 7) relative muzzle length short to moderate (UDL < 55% of UTRL); 8) cement layer thin on deciduous premolars and thick on permanent cheek teeth; 9) P3–M2 protocone occlusal outlines oval (ratio of PRL to PRW = 1.2–2.0); 10) P2–4 protocones connect with protolophs in early moderate wear and M1–2 protocones connect with protolophs in early to early moderate wear; 11) upper cheek teeth metastyles common but not well developed; 12) M1–2 protocones connect with hypocones in late wear; 13) P2 anterostyle large and unexpanded; 14) P2–M3 plis caballin well developed, single, and relatively persistent; 15) P2–M3 external and internal fossette plications simple and relatively nonpersistent; 16) P2–M3 hypoconal grooves close in moderate to late wear; 17) P3–M2 hypoconal lakes do not form with closure of hypoconal grooves; 18) dp1 very rarely present, vestigial if present; 19) dp3–4 and p3–m3 protostylids absent or may be present only near base of crowns as anterior cingulids; 20) p3–m3 metaconids and metastylids well separated only in very early to early wear; 21) p2 ectoflexid moderately deep, partially penetrates isthmus between metaconid and metastylid; 22) p3–4 ectoflexids deep, completely penetrate isthmuses between metaconids and metastylids; 23) p3–4 metastylids and metaconids equal or subequal in size and m1–3 metastylids and metaconids are equal or subequal in size and position of their lingual borders; and 24) feet tridactyl.

ETYMOLOGY. *Acritos*, Greek for mixed or

confused, in reference to morphological similarities to both equines and hipparionines; *Hippos,* Greek for horse.

DISCUSSION. Hulbert (1988b, 1989) and Kelly and Lander (1988b) recognized that "*Merychippus*" *isonesus* and "*Merychippus*" *tertius* represent a distinct clade of Neogene hypsodont horses. Downs (1956) regarded "*M.*" *isonesus* as a junior synonym of "*Merychippus*" *seversus* (= *Stylonus seversus* Cope, 1879). Accepting Downs's (1956) synonymy of "*M.*" *isonesus* with "*M.*" *seversus* and recognizing that these taxa represent a distinct clade not referable to *Merychippus s.s.,* Kelly and Lander (1988b) assigned them to *Stylonus.* However, Hulbert and MacFadden (1991) noted that *S. seversus* represents a different species from "*M.*" *isonesus* and rejected their synonymy. I now agree with Hulbert and MacFadden (1991) that these two horses are not synonymous and, furthermore, regard the holotype of *S. seversus,* an isolated upper molar (AMNH 8180), as specifically indeterminate. Therefore, *S. seversus* is a *nomen dubium* and, because of the invalidity of the species, *Stylonus* is also a *nomen dubium.*

Although Hulbert (1988b, 1989) and Kelly and Lander (1988b) recognized "*Merychippus*" *isonesus* and "*Merychippus*" *tertius* as a distinct clade, they also included "*Merychippus*" *sejunctus* (Cope, 1874) in this clade. Hulbert and MacFadden (1991) demonstrated that "*M.*" *sejunctus* and its anagenetic ancestor "*Merychippus*" sp. near "*M.*" *sejunctus* do not form a monophyletic clade with "*M.*" *isonesus* and "*M. tertius* but, instead, represent a separate clade of probable generic rank. Based on their cladistic analysis, Hulbert and MacFadden (1991) provisionally included the "*M.*" *isonesus–tertius* clade in the Hipparionini but noted other slightly less parsimonious phylogenetic arrangements, wherein the "*M.*" *isonesus–tertius* clade was the sister group of the Equini plus Hipparionini, the sister group of the protohippines plus the Hipparionini, or the sister group of the pliohippines. The cladistic analyses presented below also indicate that the "*M.*" *isonesus–tertius* clade is monophyletic and represents a generically distinct group of horses. Based on the cladistic analysis presented below and those of Hulbert (1989) and Hulbert and MacFadden (1991), "*M.*" *isonesus*, "*M.*" *tertius,* and the new species described below are herein assigned to *Acritohippus* n. gen.

Acritohippus is derived relative to *Pliohippus s.s.* by having the following character states: 1) the malar fossa is confluent with the DPOF; 2) the relative PBL is much narrower; 3) the P2–M3 internal fossette plications are slightly more complex and resistant to wear; 4) the plis caballin are better developed; and 5) the connection of the protocones to the protolophs occurs in later wear. Additional characters exhibited by *Acritohippus* that distinguish it from *Pliohippus s.s.* are as follows: 1) the cement on the deciduous premolars is thinner; 2) the dP1 is less reduced; 3) the upper cheek teeth are less curved and less hypsodont; 4) the hypoconal grooves close at a later wear stage and hypoconal lakes do not form with closure of the grooves; 5) the p2–4 ectoflexids are deeper, penetrating the isthmuses between the metaconids and metastylids; and 6) the m1–3 metastylids are about equal in size and position. The above distribution of character states clearly indicates that *Acritohippus* represents a separate genus from *Pliohippus s.s.*

Although *Acritohippus* exhibits some morphological similarities to other pliohippines and the "*Merychippus*" sp. near "*M.*" *sejunctus* clade, it can be easily distinguished from them. *Acritohippus* differs from *Parapliohippus* by having the following characters: 1) a DPOF pocket is commonly lacking and if present it is relatively shallow in depth; 2) the malar fossa is shallow in depth, crescent-shaped, and confluent with the DPOF; that is, the DPOF and the malar fossa are only separated posteriorly by a low, indistinct ridge; 3) the relative muzzle length is short to moderate (UDL < 55% of UTRL); 4) the cement layer on the deciduous cheek teeth is moderately thick; 5) the P3–M2 protocones connect with the protolophs in early moderate wear; 6) the P2–M3 plis caballin are well developed and relatively persistent; 7) the P2–M3 internal fossettes have simple plications but are slightly more complex and persistent relative to those of *Parapliohippus*; 8) P3–4 hypoconal lakes do not form with closure of the hypoconal grooves; 9) the m1–3 metastylids and metaconids are equal or subequal in size and position of their lingual borders; and 10) the UTRL is moderate (105–140 mm). *Acritohippus* differs from *Heteropliohippus* by having the following characters: 1) the malar fossa is confluent with the DPOF; 2) the P3–M3 protocones connect with the protolophs in later wear; 3) the P2–M3 plis caballin are much better developed and relatively persistent; 4) the P3–M3 internal fossette plications have simple plications but are more complex and persistent relative to those of *Heteropliohippus*; 5) the P2–M2 hypoconal grooves close in later wear; 6) the p3–m3 protostylids are absent or weakly developed; and 7) the p3–4 ectoflexids are deeper and completely penetrate the isthmuses between the metaconids and metastylids. *Acritohippus* differs from "*Merychippus*" sp. near "*M.*" *sejunctus,* a separate clade of probable generic rank, by having the following characters: 1) the relative muzzle length is shorter (UDL < 55% of UTRL); 2) the connection of the P3–4 protocones to the protolophs occurs in later wear; 3) the P3–M3 internal fossette plications are simpler and less persistent; 4) the p3–m3 protostylids are absent, or when present are much less developed; and 5) the p3–m3 metaconids and metastylids are less well separated.

Acritohippus quinni new species

Figure 3, Tables 4–6

Merychippus sumani Merriam, in part, Gazin, 1930 (pp. 50, 62, 69–72, figs. 2–4).

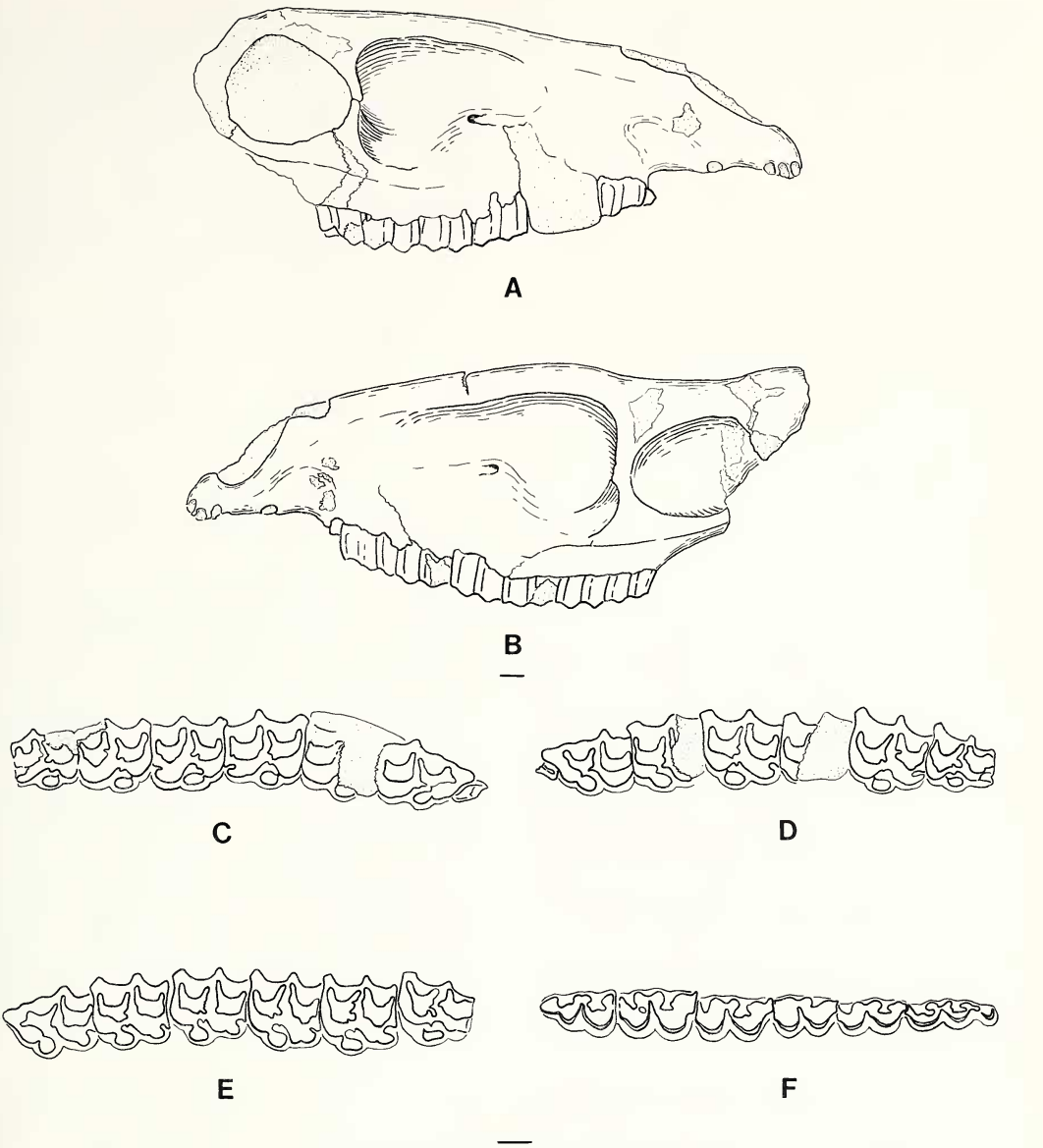

Figure 3. *Acritohippus quinni* n. gen. and sp. **A–D**, Holotype, UCMP 65338: **A–B**, partial skull, right and left lateral views; **C**, RdP1, P2–M3, occlusal view; **D**, broken LdP1, P2–M3, occlusal view. **E**, LP2–M3, UCMP 50750, occlusal view. **F**, Lp2–m3, LACM 134493, occlusal view. Scale for A–B = 10 mm, C–F = 10 mm.

Merychippus sumani Merriam, in part, James, 1963 (pp. 12, 19, 26–27, tab. 2).
"*Merychippus*" cf. "*M.*" *stylodontus* (Merriam) Woodburne *vide* Bernor *et al.*, 1980.
"*Pliohippus*" sp. J.P. Quinn, 1984 (pp. 199–209, figs. 48–50, tab. 6).
"*Merychippus*" n. sp. J.P. Quinn, 1987 (pp. 23, 27, tab. 1).
Stylonus n. sp. Kelly and Lander, 1988b (p. 4), 1992 (p. 3, appendix 1).

HOLOTYPE. Partial skull with RdP1, RP2, partial RP3, RP4–M3 and partial LP2, LP3, partial LM1, LM2–3, UCMP 65338.

TYPE LOCALITY. UCMP V-5823.

DIAGNOSIS. *Acritohippus quinni* differs from *A. isonesus* and *A. tertius* by having the following characters: 1) larger size (mean UTRL = 127.3 mm); 2) deeper DPOF (> 15 mm); 3) shorter relative muzzle length (UDL = 32% of UTRL); 4) more hypsodont cheek teeth (about 35 mm); and 5) less curvature of upper cheek teeth (ROC = 45–50 mm). Further differs from *A. isonesus* by having the following characters: 1) DPOF with deeper posterior pocket (> 5 mm); 2) P2–M2 hypoconal grooves close in earlier wear stage; and 3) P2–M3 fossette plications slightly less developed. Further differs from *A. tertius* by having DPOF posteriorly pock-

Table 4. Measurements (in mm) of upper dentition of holotype of *Acritohippus quinni* n. sp. from the Caliente Formation. a = approximate.

Dimension		Right	Left
P2	A-P	25.6	25.7
	TR	21.2	21.4
P3	A-P	22.2a	—
	TR	24.8	—
P4	A-P	22.4	22.6
	TR	24.6	24.5
M1	A-P	—	19.5
	TR	—	22.7
M2	A-P	21.1	21.3
	TR	21.1a	21.7
M3	A-P	20.9	20.3a
	TR	19.6	20.1
P2–4	APL	69.3	69.5
M1–3	APL	61.8	61.5
P1–M3	APL	—	135.5
UTRL		127.2	127.0

eted and M1–2 protocones connecting with protolophs in later wear stage.

ETYMOLOGY. Named in honor of James Patrick Quinn, a research associate of the Natural History Museum of Los Angeles County, who first recognized the distinctive characters of this species.

REFERRED SPECIMENS. Partial skull with RP2–M3 and LP2–M3, UCMP 52525; associated partial skull with RP2–M3 and LP2–M3, right and left dentaries with i1–m3, and appendicular elements, UCMP 51000; partial left maxilla with P2–M3, UCMP 50667; partial left maxilla with P2–M3, UCMP 50750; partial left maxilla with P2–M3 and associated right dentary with p2–m3, UCMP 50950; partial left maxilla with P4–M3, UCMP 51180; partial right maxilla with dP1 and P2–M3, UCMP 51300; partial right dentary with p3–m3, UCMP 50680; associated partial dentaries with Ri2–m3 and Li1–m3, UCMP 51230; associated partial dentaries with Rc–i1 and Li1–m3, UCMP 51260; partial right dentary with p2–m3, UCMP 52525; partial skull with RdP1, P2–M3, and LP2–M3, LACM 15625; skull with RdP4, M1–2, and partial LdP3–4 and M1–2, LACM 134495; associated partial dentaries with Rp3–m3 and Lp2–m3, LACM 134493; associated partial dentaries with Rp3–m3 and Lp2–m3, LACM 138112; partial left dentary with p2–m3, LACM 138075.

DISTRIBUTION AND AGE. California: West Dry Canyon, Lower Dome Spring, Upper Dome Spring, and Doe Spring Canyon Local Faunas, Caliente Formation, Cuyama Valley Badlands, latest Hemingfordian to late Barstovian; "*Merychippus*" cf. "*M.*" *intermontanus* Range Zone, Bopesta Formation, southern Sierra Nevada, late Barstovian.

DESCRIPTION. The facial morphology is well preserved in several skulls and is characterized by a moderately deep, posteriorly pocketed DPOF that is confluent with the malar fossa; that is, the DPOF and the malar fossa are only separated posteriorly by a low, rounded, indistinct ridge (Figures 3A–3B). The preorbital bar between the DPOF and the orbit is very narrow (6 mm). The buccinator fossa is a moderately developed depression on the anterior maxilla and is separated posterodorsally from the DPOF by a very low, indistinct ridge. The facial crest is dorsoventrally compressed. The rostrum is relatively short with the C–P2 diastema about 23–32 mm in length.

The DPOF is characterized by having the following: 1) the dorsal margin is formed by a distinct, rounded rim; 2) the posterior margin is formed by a distinct, sharply edged rim; 3) the anteroventral margin is confluent with the face and somewhat constricted by a lateral expansion of the face above the P4–M1; 4) the posteroventral margin is formed

Table 5. Summary of measurements (in mm) of upper dentition of *Acritohippus quinni* n. gen. and sp. from the Caliente Formation.

Dimension		N	OR	Mean	SD	CV
P2	APL	7	23.6–26.7	25.1	1.4	5.4
	TR	7	19.2–22.3	20.5	1.2	5.8
P3	APL	5	21.6–23.2	22.3	0.7	3.2
	TR	6	20.6–24.8	22.7	1.5	6.7
P4	APL	8	20.4–22.5	21.9	0.7	3.4
	TR	7	22.2–24.6	23.2	0.9	3.6
M1	APL	7	19.4–20.7	20.2	0.6	3.2
	TR	8	21.9–24.7	22.9	0.9	4.1
M2	APL	7	20.0–21.2	20.6	0.4	2.0
	TR	8	20.6–23.6	22.0	1.0	4.4
M3	APL	7	20.5–22.3	21.0	0.7	2.9
	TR	7	19.1–21.7	20.0	0.8	4.0
P2–4	APL	5	61.3–74.1	68.9	4.7	6.8
M1–3	APL	5	59.5–64.4	61.4	2.0	3.3
P1–M3	APL	1	135.5			
UTRL		4	125.2–130.4	127.3	—	—

Table 6. Summary of measurements (in mm) of lower dentition of *Acritohippus quinni* n. gen. and sp. from the Caliente Formation.

Dimension		N	OR	Mean	SD	CV
p2	APL	7	20.5–22.4	22.1	1.2	5.6
	TR	7	10.9–12.4	11.7	0.6	5.1
p3	APL	10	19.4–22.5	21.6	1.0	4.7
	TR	8	12.0–13.9	13.1	0.8	5.7
p4	APL	11	20.2–22.7	21.8	1.4	6.5
	TR	10	11.9–13.4	12.8	0.6	4.4
m1	APL	10	19.4–22.6	20.8	1.3	6.1
	TR	11	10.6–12.6	11.7	0.7	5.7
m2	APL	12	19.1–23.0	21.5	1.4	6.5
	TR	12	10.0–11.2	10.6	0.6	5.5
m3	APL	10	23.2–25.4	24.5	0.9	3.5
	TR	11	8.5–10.6	9.4	0.8	8.0
p2–4	APL	8	61.5–66.7	65.0	2.1	3.2
m1–3	APL	12	61.0–66.8	64.5	2.3	3.6
p2–m3	APL	9	120.3–133.2	128.6	4.9	3.8

by a low, indistinct, rounded ridge; 5) the shape is elongate oval; 6) the depth is moderately deep (> 15 mm); and 7) the posterior aspect is pocketed (6–8 mm deep).

The malar fossa is characterized by the following: 1) the ventral and posterior margins are bounded by distinct ridges; 2) the dorsal margin is formed by the low, indistinct ridge separating it from the DPOF; 3) the anterior margin is confluent with the face; 4) the depth is shallow (about 5 mm deep); and 5) it is not pocketed posteriorly.

The deciduous P1 is always present and moderate in size. The deciduous P2–4 are similar to the adult premolars except that the morphology of occlusal outlines of the fossette plications is less complex, the plis caballin less persistent, and the protocones connect with the protolophs at an earlier wear stage.

The permanent upper premolars and molars are characterized by the following (Figures 3C–3E): 1) the cement layer is moderately thick; 2) the curvature is moderate; 3) the mesostyles are distinct but not prominent; 4) the internal fossette plications are simple with the pli protoconule and pli prefossette single and relatively nonpersistent; 5) the external fossette plications are very simple with very poorly developed single plis protoloph that are nonpersistent and lacking plis hypostyle; 6) the plis caballin are single, moderately well developed, and relatively persistent; 7) the protocones have oval occlusal outlines with small anterolabial spurs in very early wear and connect with the protolophs in early moderate wear; that is, the M1 protocone is connected when the M3 is in early wear; 8) the hypocones are relatively distinct forming round to slightly elongated occlusal outlines in early wear; and 9) the hypoconal grooves are relatively persistent and close without forming hypoconal lakes in moderate wear.

The dp1 is usually absent but, when present, is vestigial. The lower premolars and molars are characterized by the following (Figure 3F): 1) the cement layer is moderately thick; 2) the metaconids and metastylids are only well separated in early wear and the metastylids and metaconids are equal or subequal in size and position of their lingual borders; 3) the preflexids and postflexids have simple margins and, with wear, become widely separated with the labial depth of the preflexid very shallow; 4) the m1–3 plis caballinid are commonly present in early to moderate wear as small indentations; and 5) the p2 ectoflexid is moderately deep and partially penetrates the isthmus between the metaconid and metastylid, whereas the p3–m3 ectoflexids are deep, completely penetrating the isthmuses between the metaconids and metastylids.

The measurements of the teeth of *Acritohippus quinni* are presented in Tables 4–6.

DISCUSSION. Hulbert and MacFadden (1991) suggested that the late Hemingfordian *Acritohippus tertius* and the early Barstovian *Acritohippus isonesus* may represent endpoints in a morphocline, wherein *A. tertius* gave rise to *A. isonesus* by anagenetic speciation. Furthermore, they noted that these taxa could eventually be synonymized if this relationship is confirmed by further study. Even if *A. tertius* is eventually proven to be a junior synonym of *A. isonesus*, *Acritohippus quinni* cannot be regarded as synonymous with *A. isonesus* because of the following facts: 1) *A. quinni* exhibits at least seven apomorphic character states relative to *A. isonesus* (see Diagnosis above); 2) both *A. isonesus* and *A. quinni* existed during the same chronologic interval, the early to late Barstovian; and 3) each species appears to have been geographically isolated, with *A. quinni* known only from southern California and *A. isonesus* known primarily from the Northwest and Midwest. A more probable scenario is that the Hemingfordian *A. tertius* or a similar plesiomorphic ancestor gave rise to a southern West Coast population that evolved

into *A. quinni* and a more northern population that evolved into *A. isonesus*. This scenario is also supported by the observations of MacFadden and Hulbert (1988), Hulbert and MacFadden (1991), and MacFadden (1992) that, during the late Hemingfordian and early Barstovian of North America, hypsodont horses underwent an explosive adaptive radiation, in which many equid faunas exhibited distinct regional endemism.

COMPARATIVE REEVALUATION OF *PLIOHIPPUS S.S.*

Pliohippus s.s. exhibits similarities in certain facial and dental morphologies with *Parapliohippus, Astrohippus, Heteropliohippus, Acritohippus,* and "*Merychippus*" *stylodontus* (a monophyletic clade of probable generic rank). In order to discuss the relationships of *Pliohippus s.s.* to these taxa, a review of *Pliohippus* is presented here. Marsh (1874, p. 252) originally named *Pliohippus* based on *Pliohippus pernix* from the "Pliocene sands of the Niobrara River, Nebraska." In his diagnosis, he differentiated *Pliohippus* from *Protohippus* and *Equus* as follows: 1) *Pliohippus* differs from *Protohippus* by the "absence of lateral digits, which are only represented by slender splint bones"; and 2) *Pliohippus* differs from *Equus* by "the presence of a large antorbital fossa, a functional upper first premolar, and by a different composition of the crowns of the upper molars." Marsh's only additional reference to the facial morphology of *Pliohippus pernix* was that it possesses a "deep irregular fossa in front of the orbit." Additional characters cited in his description of *Pliohippus pernix* were as follows: "the molar teeth have very short crowns, the folds of the enamel are very simple and there are none in the inner lobes, the ungual phalanges are broad, the femur has the fossa above its outer condyle unusually deep, and the cuboid facet on the astragalus is larger than most equines." Gidley (1907) noted that Marsh (1874) founded *Pliohippus* primarily on the absence of lateral digits. Gidley (1907, p. 868) regarded *Pliohippus* as closely related to *Protohippus,* based on the shared character state of having the "protocones and hypocones partially or completely connected to the protolophs and metalophs," respectively. However, Gidley (1907, pp. 868, 894) further noted that *Pliohippus* differs from typical *Protohippus* by having "a large lachrimal fossa" and "a deep malar pit that is apparently wanting in *Protohippus.*" Osborn (1918) revised *Pliohippus* and listed 12 defining character states for the genus. Although Osborn (1918) recognized *Pliohippus pernix* as the genotype, he also assigned species to *Pliohippus* that are now referred to *Equus, Protohippus, Dinohippus s.s.,* and "*Dinohippus*" (e.g. *Equus simplicidens* [Cope, 1892], *Equus cumminsii* Cope, 1893, *Protohippus supremus* Leidy, 1869, *Dinohippus leidyanus* [Osborn, 1918], "*Dinohippus*" *spectans* [Cope, 1880], and "*Dinohippus*" *interpolatus*). Nevertheless, the following derived character states listed by Osborn (1918) still are regarded by many investigators as typical for *Pliohippus*: 1) a malar fossa is present; 2) the upper cheek teeth are hypsodont and strongly curved; 3) the protocones are oval in shape and connect with the protolophs in very early wear; and 4) the fossettes are simple with few plications of the enamel borders. However, each of these character states also is present in other equid genera. For example, *Astrohippus* (MacFadden 1984b) and *Acritohippus* possess a malar fossa, and *Dinohippus* possesses upper cheek teeth that have relatively strong curvature, simple fossettes, and oval to elongated oval protocones that connect with the protolophs in very early wear (J.H. Quinn, 1955; MacFadden, 1984b). Therefore, rather than representing autapomorphies of *Pliohippus,* the above character states represent synapomorphies uniting *Pliohippus* with certain other genera of the Equinae.

Hulbert (1989, 1993) and Hulbert and MacFadden (1991) regarded *Pliohippus s.s.* as being characterized by a monophyletic lineage including *Pliohippus mirabilis* (Leidy, 1858) (= *Pliohippus campestris* [Gidley, 1907]), *Pliohippus pernix* (= *Pliohippus robustus* Marsh, 1874, *Pliohippus pachyops* [COPE, 1893], *Pliohippus lullianus* Troxell, 1916), and *Pliohippus nobilis* Osborn, 1918. They considered these species to represent a single lineage, wherein the middle to late Barstovian *Pliohippus mirabilis* gave rise by anagenetic speciation to the Clarendonian *Pliohippus pernix,* which then gave rise by anagenetic speciation to the early Hemphillian *Pliohippus nobilis.* Additional species referable to *Pliohippus s.s.* are as follows: 1) *Pliohippus fossulatus* (Cope, 1893), a derived species that exhibits a very deep compartmentalized malar fossa (Stirton and Chamberlain, 1939; MacFadden 1984b; Hulbert, 1989); and 2) *Pliohippus tantalus* (Merriam, 1913b) (= *Pliohippus fairbanksi* Merriam, 1915), a West Coast species whose facial and dental morphology are very similar to *Pliohippus pernix* (Merriam, 1913b, 1915, 1919; Vanderhoof, 1933; Hulbert, 1988a). *Pliohippus s.s.,* as typified by *Pliohippus pernix* and characterized by the above monophyletic lineage, exhibits the following combination of derived character states relative to the outgroup "*Parahippus*" *leonensis* and based on the cladistic analyses presented below: 1) a DPOF that is pocketed and distinctly rimmed posteriorly and a malar fossa that is deep, pocketed posteriorly, and well separated from the DPOF by a distinct ridge of bone; 2) a posteriorly positioned infraorbital foramen, about below the middle of the P4; 3) a moderate relative PBL (ratio of PBL to UTRL = 0.10–0.20); 4) thick cement on the deciduous premolars; 5) moderate reduction of the dP1 (ratio of dP1 APL to P2 APL about 0.30); 6) strongly curved upper cheek teeth (ROC > 40 mm, secondarily derived); 7) hypsodont upper cheek teeth (M1 unworn crown height > 50 mm); 8) hypoconal lakes form with closure of the P2–4 hypoconal

grooves; 9) hypoconal lakes form with closure of the M1–2 hypoconal grooves; 10) very simple internal fossette plications that commonly disappear with wear; 11) reduced plis caballin; 12) connection of the protocones to the protolophs occurs in very early wear; 13) connection of the protocones to the hypocones occurs prior to late wear; 14) closure of the hypoconal grooves occurs in early wear; 15) moderate depth of the p2–4 ectoflexids, only partially penetrating the isthmuses between the metaconids and metastylids; and 16) the m1–3 metastylids are notably smaller and positioned more labially than the metaconids.

Parapliohippus, Astrohippus, Acritohippus, Heteropliohippus, and "*Merychippus*" *stylodontus* all possess a DPOF and malar fossa, but the fossa morphology in each of these taxa differs from *Pliohippus s.s.* as follows (hypothesized polarity of each character state included in parentheses): 1) *Parapliohippus* differs by having the DPOF extensively developed posteriorly, resulting in the effective removal of the lacrimal bone from the fossa, except at the orbital rim (apomorphic), whereas in *Pliohippus s.s.* the lacrimal bone is not reduced anteriorly and extends well into the DPOF; 2) *Astrohippus* differs by having a large unpocketed DPOF that is indistinctly separated from a large shallow unpocketed malar fossa, which commonly contains small concentric pits, and a very faint dorsoventral bar that divides these fossae into anterior and posterior portions (apomorphic); 3) *Acritohippus* differs by having a small, but distinct, shallow unpocketed malar fossa that is confluent with the DPOF; that is, the fossae are only separated posteriorly by a very low, indistinct ridge (apomorphic); 4) *Heteropliohippus* differs by having an unpocketed DPOF with a distinct anterior rim and a small, shallow, unpocketed malar fossa (apomorphic reversal); and 5) "*M.*" *stylodontus* differs by having an unpocketed DPOF and a shallow unpocketed malar fossa (plesiomorphic).

In addition to the differences in facial fossa morphology, each of these taxa exhibit a distinct combination of character states that differs from the combination of derived character states listed above for *Pliohippus s.s. Parapliohippus* exhibits the following distribution of character states relative to the 16 derived character states listed above for *Pliohippus s.s.*: 1) plesiomorphic for character state numbers 2, 4, 5, 7, 9, 13, 14, and 15 and 2) synapomorphic for character state numbers 1, 6, 8, 10, 12, and 16. Derived character states exhibited by *Parapliohippus* relative to *Pliohippus s.s.* are as follows: 1) extensive posterior development of the DPOF with the anterior aspect of lacrimal bone reduced; 2) a narrow relative PBL (ratio of PBL to UTRL about 0.05); 3) the protolophs and metalophs remain separate until the teeth are more than 50% worn; and 4) small size (UTRL = 90–100 mm). *Astrohippus* exhibits the following distribution of character states relative to the 16 derived character states listed above for *Pliohippus s.s.*: 1) plesiomorphic for character states 8 and 9 and 2) synapomorphic for character states 4, 7, 10, 12, and 14. Derived character states exhibited by *Astrohippus* relative to *Pliohippus s.s.* are as follows: 1) a distinctive DPOF and malar fossa morphology (see above); 2) the infraorbital foramen is positioned farther posteriorly, about below posterior half of P4 to M1; 3) the relative PBL is narrow (ratio of PBL to UTRL about 0.08); 4) the upper cheek teeth are relatively straight (secondarily derived); 5) plis caballin are usually absent; 6) the protocones and hypocones connect only in late wear; 7) the P2–M2 hypoconal grooves close in early wear; 8) the p2–4 ectoflexids are shallow, not penetrating the isthmuses between the metaconids and metastylids; and 9) the m1–3 metaconids and metastylids are about equal in size and position (secondarily derived). *Acritohippus* exhibits the following distribution of character states relative to the 16 derived character states listed above for *Pliohippus s.s.*: 1) plesiomorphic for character states 4, 5, 6, 7, 8, 9, 13, 14, 15, and 16 and 2) synapomorphic for character state 2. Derived character states exhibited by *Acritohippus* relative to *Pliohippus s.s.* are as follows: 1) a distinctive DPOF and malar fossa morphology (see above); 2) a narrow relative PBL (ratio of PBL to UTRL about 0.05); 3) simple, but persistent, internal fossette plications; 4) moderately well-developed plis caballin; and 5) the connection of the protocones to the protolophs occurs in early moderate wear. *Heteropliohippus* exhibits the following distribution of character states relative to the 16 derived character states listed above for *Pliohippus s.s.*: 1) plesiomorphic for character states 5, 6, 7, 8, 9, and 12 and 2) synapomorphic for character states 4, 10, 11, 14, and 15. Derived character states exhibited by *Heteropliohippus* relative to *Pliohippus s.s.* are as follows: 1) a distinctive DPOF and malar fossa morphology (see above); 2) the relative PBL is narrow (ratio of PBL to UTRL about 0.08); 3) the infraorbital foramen is positioned posteriorly, about below M1; 4) the upper cheek teeth are moderately curved; 5) the p3–m3 protostylids are moderately developed; and 6) the m1–3 metaconids and metastylids are about equal in size and position (secondarily derived). "*Merychippus*" *stylodontus* exhibits the following distribution of character states relative to the 16 derived character states listed above for *Pliohippus s.s.*: 1) plesiomorphic for character states 6, 7, 8, 9, and 15 and 2) synapomorphic for character states 2, 5, 10, 11, 13, 14, and 16. Derived character states exhibited by "*M.*" *stylodontus* relative to *Pliohippus s.s.* are as follows: 1) an extremely narrow relative PBL (ratio of PBL to UTRL about 0.035), and 2) the connection of the protocones to protolophs occurs in early wear.

In summary, *Pliohippus s.s.* is derived relative to *Parapliohippus* in at least 8 character states, derived relative to *Astrohippus* in at least 5 character states, derived relative to *Acritohippus* in at least 11 character states, derived relative to *Heteropliohippus* in

at least 7 character states, and derived relative to "*Merychippus*" *stylodontus* in at least 6 character states. *Parapliohippus* is derived relative to *Pliohippus s.s.* in at least four character states and derived relative to *Astrohippus, Acritohippus, Heteropliohippus,* and "*M.*" *stylodontus* in at least three character states. *Astrohippus* is derived relative to *Pliohippus s.s.* and *Acritohippus* in at least 9 character states, derived relative to *Parapliohippus* in at least 11 character states, derived relative to "*M.*" *stylodontus* in at least 8 character states, and derived relative to *Heteropliohippus* in at least 3 character states. *Acritohippus* is derived relative to *Pliohippus s.s., Parapliohippus,* "*M.*" *stylodontus,* and *Heteropliohippus* in at least five character states and derived relative to *Astrohippus* in at least four character states. "*Merychippus*" *stylodontus* is derived relative to *Pliohippus s.s., Parapliohippus, Astrohippus, Acritohippus,* and *Heteropliohippus* in at least two character states. *Heteropliohippus* is derived relative to *Pliohippus s.s.* in at least six character states, derived relative to *Parapliohippus, Acritohippus,* and "*M.*" *stylodontus* in at least four character states, and derived relative to *Astrohippus* in at least three character states. These comparisons clearly demonstrate that paraphyly would result if any of the other taxa (*Parapliohippus, Astrohippus, Acritohippus, Heteropliohippus,* "*M.*" *stylodontus*) were assigned to *Pliohippus s.s.*

In conclusion, all of the above data and the cladistic analyses presented below and those of Hulbert (1989) and Hulbert and MacFadden (1991) clearly justify recognizing *Parapliohippus, Heteropliohippus,* and *Acritohippus* as generically distinct from *Pliohippus s.s.* and all other genera of the Equinae. "*Merychippus*" *stylodontus* also appears to represent a generically distinct clade. However, erecting a new genus for "*M.*" *stylodontus* does not seem prudent because it exhibits only two derived character states relative to *Pliohippus s.s., Parapliohippus, Heteropliohippus,* and *Acritohippus.* Furthermore, as noted above, it is plesiomorphic for at least five character states relative to *Pliohippus s.s.* If future discoveries result in the identification of additional apomorphic character states for "*M.*" *stylodontus,* then establishing a new genus would be warranted. However, until such time, I regard "*M.*" *stylodontus* as a plesion of generic rank.

PHYLOGENETIC SYSTEMATICS OF NEOGENE HYPSODONT HORSES

In recent years, several investigators have used cladistic analyses to clarify the systematics of the North American Neogene hypsodont horses (e.g. MacFadden, 1984a; Webb and Hulbert, 1986; Hulbert, 1987a, 1988a, 1988b, 1989; MacFadden and Hulbert, 1988; Evander, 1989; Hulbert and MacFadden, 1991). In particular, the cladistic analyses presented by Hulbert (1987a, 1989) and Hulbert and MacFadden (1991) have provided many insights regarding the phylogenetic relations of Neogene hypsodont horses. Hulbert (1989) analyzed a large number of late Neogene horse taxa, whereas Hulbert and MacFadden (1991) restricted their analysis to critical taxa involved in the basal Miocene radiation of hypsodont horses. Based primarily on these two analyses, Hulbert and MacFadden (1991, figs. 13, 17) and Hulbert (1993, fig. 1) proposed the most significant vertical phylogenetic reevaluation of these horses to date.

Most of the character states that Hulbert (1988b, 1989) and Hulbert and MacFadden (1991) listed for the various equid genera appear valid, but a few require additional discussion. Hulbert (1987b) regarded all hipparionine genera as being united based on the following synapomorphies: 1) the metastylids are subequal or equal in size to the metaconids; 2) the entoflexids, metaflexids, and linguaflexids are well developed and isolate the metaconids and metastylids from each other; and 3) the deciduous premolars have a thick coat of cement. Hulbert (1988b) suggested that *Acritohippus tertius, Acritohippus isonesus,* and "*Merychippus*" *sejunctus* form a monophyletic group with the following synapomorphies uniting them: 1) more isolated protocones; 2) increased size; and 3) well-developed metastyles. Hulbert (1988b) listed five ancestral synapomorphies that unite "*M.*" *sejunctus* with the Hipparionini. However, according to his own listed character states for "*M.*" *sejunctus* (Hulbert, 1988b, tab. 9), only two are actually shared by "*M.*" *sejunctus* and the Hipparionini: 1) strong plis caballin on the upper molars and 2) metacarpal V articulates primarily with metacarpal IV. In a much more comprehensive cladistic analysis of late Neogene horses, Hulbert (1989) stated that the only apomorphy that unites the Hipparionini is a well-separated metaconid and metastylid and that *A. isonesus* and "*M.*" *sejunctus* possess this character state. However, Hulbert (1988b) clearly stated that "*M.*" *sejunctus* has the metaconid and metastylid well separated only in early wear (Hulbert, 1988b, tab. 9, character state 55.1), which is also the same plesiomorphic character state he listed for the Equini and "*Merychippus*" *primus.* Furthermore, my examination of lower dentitions referred to *A. isonesus* from the Mascall Formation (Oregon), Sucker Creek Formation (Oregon), and High Rock Sequence (Nevada) does not support *A. isonesus* as having the derived state but, instead, the plesiomorphic state of being well separated only in early wear. Hulbert and MacFadden (1991) regarded "*M.*" *sejunctus* as being anagenetically derived from the early Barstovian "*Merychippus*" sp. near "*M.*" *sejunctus* of Texas, and they clearly indicated that it exhibited the hipparionine characters of well-developed plis caballin, moderately complex fossette margins, and well-separated metaconids and metastylids.

Hulbert (1988a) considered the synapomorphic characters that unite the Equini to be the following: 1) the protocones connect to the protolophs in very early wear stages; 2) the internal fossette plications

have relatively simple margins; and 3) the lower molar metastylids are positioned more labially than the metaconids. Later, Hulbert (1989) regarded the labially positioned lower molar metastylids as the only apomorphy uniting the Equini. Hulbert (1989) placed *Parapliohippus carrizoensis* and "*Merychippus*" *stylodontus* in plesions (plesiomorphs) within the *Equus* genus group of the Equini, with each taxon having the following synapomorphies: 1) the malar fossa is present and well separated from the DPOF; and 2) the p3–m3 protostylids are absent. Hulbert (1989) also considered *P. carrizoensis* as being united with all other members of the *Equus* genus group by having the following synapomorphies: 1) the DPOF is pocketed posteriorly; and 2) the protocones connect with the protolophs immediately after the onset of wear. Hulbert (1989) regarded *P. carrizoensis* as being derived relative to other members of the *Equus* genus group by having the following synapomorphies: 1) a very narrow PBL; and 2) small size. In my examination of specimens referred to *P. carrizoensis* and "*M.*" *stylodontus,* I have found the following: 1) *P. carrizoensis* and "*M.*" *stylodontus* occasionally have the plesiomorphic character state of small anterior cingulids or precingulids that extend only partially up the anterior labial face of the lower cheek teeth; and 2) "*M.*" *stylodontus* has lower molar metastylids and metaconids that are well separated only in early wear.

Hulbert and MacFadden (1991) and MacFadden (1992) regard the character state of having the m1–2 metastylids notably smaller and located more labially than the metaconids as one of the synapomorphies that unite the Equini (Protohippina plus Equina). Hulbert (1988a, tab. 18) noted that in early species of *Calippus* and *Protohippus* the metaconids and metastylids are only well separated in early wear and that the evolution of increased protocone length and a corresponding increased MML occurred independently within these two lineages. Furthermore, Hulbert (1988a, p. 285, tab. 17) also noted that the Barstovian *Protohippus perditus* (Leidy, 1858), and *Protohippus supremus,* exhibit the character state of having the metastylids only slightly smaller or equal in size to the metaconids, respectively. Rensberger *et al.* (1984) concluded that an increase in anteroposteriorly directed enamel edges occurred in Neogene hypsodont horse teeth as a functional response to diet, maximizing anteroposterior grinding, and this response can be observed in such diverse genera as *Neohipparion* and *Equus.* Hulbert (1988a) suggested that this functional response may explain the observed trend in protohippine and equine genera, wherein as the protocone increases in length there is a corresponding enlargement of the metaconid–metastylid complex. This trend also is observed in the hipparionines, *Neohipparion, Cormohipparion,* and *Pseudhipparion.* These facts indicate that the morphology of the protocone and the corresponding metaconid–metastylid complex may be prone to homoplasy in response to the functional dietary requirements of a taxon and, therefore, could be independently derived within lineages depending on the feeding strategy. This is not to say that the morphology of the metaconid–metastylid complex is not useful in establishing equid relations, but it may be prone to convergence.

In recent years, the use of facial characters, in particular the morphology of the DPOF and the malar fossa, has been demonstrated to be significant in elucidating the phylogenetic relations of Neogene hypsodont horses (e.g. Skinner and MacFadden, 1977; Bernor *et al.,* 1980; Woodburne, 1982, 1989; J.P. Quinn, 1984; MacFadden, 1984a, 1984b, 1985, 1992; Hulbert, 1988a, 1988b, 1989; Kelly and Lander, 1988b; Alberdi, 1989; Hulbert and MacFadden, 1991). The presence of a well-developed malar fossa is regarded as a derived character state (Hulbert, 1989; Hulbert and MacFadden, 1991). Webb and Hulbert (1986) considered a shallow malar fossa to be a retained primitive character and noted that a vestigial malar fossa may occur occasionally in *Pseudhipparion, Calippus, Merychippus insignis* Leidy, 1857 (Skinner and Taylor, 1967), and *Neohipparion* (MacFadden, 1984a). However, Hulbert (1988a) and Hulbert and MacFadden (1991, tab. 1) stated that a malar fossa is absent in *Calippus* and *Merychippus insignis,* respectively. Hulbert (pers. commun., 1994) considers the very slight depression occasionally present in *Pseudhipparion, Calippus, Neohipparion,* and *Merychippus insignis,* which Webb and Hulbert (1986) referred to as a "malar fossa," to be presumably caused by a stronger than usual muscle attachment on the malar crest. Although possibly homologous with the malar fossa of the Equini, this slight depression, which is highly variable in its expression, cannot be equated with the derived character state of a well-developed and consistently present malar fossa, such as those of *Pliohippus s.s.* and *Acritohippus* (Hulbert, pers. commun., 1994).

In Hulbert's (1989) analysis of late Neogene hypsodont horses, he recognized the following three character states for the malar fossa: 1) absent or very shallow and variable (primitive); 2) present but not confluent with the DPOF (derived); and 3) present and confluent with the DPOF (derived). In Hulbert and MacFadden's (1991) analysis of basal Neogene hypsodont horses, they also recognized three character states for the malar fossa, but these differed as follows: 1) no malar fossa present; 2) rudimentary or shallow malar fossa present; and 3) deep malar fossa present. Although the malar fossa character states used in these two analyses overlap somewhat, they emphasize slightly different polarities. Except when character state reversal occurs, such as in *Equus* and in *Dinohippus s.s.,* the absence of a malar fossa is plesiomorphic, as indicated by its absence in the outgroup "*Parahippus*" *leonensis* (Sellards, 1916), and "*Merychippus*" *primus,* and a very shallow, variably present malar fossa

most probably is also plesiomorphic (Webb and Hulbert, 1986). Furthermore, a distinct malar fossa that is always present and confluent with the DPOF is not equivalent to the plesiomorphic state of a very shallow and variably present malar fossa. Hulbert (1989) recognized this fact and regarded this character state as being derived. Similarly, a distinct malar fossa that is confluent with the DPOF is not equivalent to one that is well separated from the DPOF. For these reasons, the malar fossa character states used in the cladistic analyses presented herein follow those of Hulbert (1989).

Hulbert and MacFadden (1991, p. 17, character 8) included the following character states for the shape of the DPOF in their cladistic analysis: "1) an elongate oval shape (the length is much greater than the height); and 2) oval shape (the length is about equal to the height)." The only taxa they recognized as having an oval-shaped DPOF were *Parapliohippus carrizoensis* and *Acritohippus tertius*. However, the DPOF in *P. carrizoensis* and the acritohippines (*A. tertius, A. isonesus,* and *A. quinni*) is about twice as long as it is high (Woodburne, pers. commun, 1994; this report). The only way to regard these taxa as having an "oval-shaped" DPOF, wherein "the length is about equal to the height," would be to include the malar fossa as contributing to the "height" of the DPOF. Therefore, I regard the DPOF shape as being an elongated oval in *P. carrizoensis* and the acritohippines. In the cladistic analyses presented herein, this character was excluded because all of the taxa analyzed possess an elongate oval-shaped DPOF.

Sondaar (1968) first noted that certain hipparionines possess the character state of metacarpal V articulating primarily with metacarpal IV, differing from certain equines in which metacarpal V primarily articulates with the unciform carpal. Hulbert and MacFadden (1991, p. 19, character 79) recognized the following character states for the articulation of metacarpal V: 1) metacarpal V articulates primarily on the unciform carpal, wherein the articulation facet for metacarpal IV is absent or smaller than the articulation facet on the unciform carpal (plesiomorphic); and 2) metacarpal V articulates primarily with metacarpal IV, wherein the articulation facet on the unciform is smaller than on metacarpal IV or absent (apomorphic). Based on their cladistic analysis, Hulbert and MacFadden (1991) regarded the derived character state for this character as one of the synapomorphies uniting the Hipparionini. However, the character state distribution for this character is unknown or has not been determined for many late Neogene horses. For example, the character state for this character is only known for 5 of the 13 taxa analyzed by Hulbert and MacFadden (1991) and 12 of the 27 taxa analyzed herein. In Eocene horses, such as *Hyracotherium, Orohippus,* and *Epihippus,* metacarpal V, although slightly reduced, supported a functional digit with three phalanges (Matthew, 1926; Kitts, 1956, 1957). When horses evolved a tridactyl manus during the early Oligocene, metacarpal V was reduced to a very small vestigial bone (Osborn, 1918; W.B. Scott, 1941; Simpson, 1951). In modern horses there is no trace of a metacarpal V (Evander, 1989). In terms of morphological function, it is difficult to explain the two different character states for the metacarpal V articulation in late Neogene horses. It could be argued that the articulation of metacarpal V should not be included in a phylogenetic analysis of late Neogene horses because metacarpal V is vestigial and its functional morphology has not been determined. Nevertheless, there does seem to be a trend in the known distribution of the articulation morphology, wherein the hipparionines exhibit the derived state and the equines exhibit the plesiomorphic state (Hulbert and MacFadden, 1991). However, this character state must be regarded as equivocal for establishing phylogenetic relationships until the character state distribution for this character is much better known.

To facilitate easy comparison of the analyses presented herein with those previously published, the numbering scheme of the characters and character states (Appendix A) generally corresponds to those of Hulbert (1988b, 1989) and Hulbert and MacFadden (1991). Except as noted above, the polarities and descriptions of all of the characters and character states presented in Appendix A have been discussed in detail by other investigators (e.g. Sondaar, 1968; Webb, 1969; Hussain, 1975; MacFadden, 1984a, 1984b, 1992; Webb and Hulbert, 1986; Hulbert, 1987a, 1988a, 1988b, 1989; Hulbert and MacFadden, 1991).

Hulbert (1989) and Hulbert and MacFadden (1991) performed their cladistic computer analyses using the PAUP algorithm (Swofford, 1985). In order to compare the Hennig86 program used herein and the PAUP program used by Hulbert (1989) and Hulbert and MacFadden (1991), the character state matrices used by Hulbert (1989) and Hulbert and MacFadden (1991) in their respective analyses were run on the Hennig86 program. The results of these two analyses were identical to those of Hulbert (1989) and Hulbert and MacFadden (1991).

Based on a synthesis of the analyses of Hulbert (1989) and Hulbert and MacFadden (1991) plus those of Hulbert (1987a, 1988a, 1988b) and Webb and Hulbert (1986), Hulbert and MacFadden (1991, fig. 13) hypothesized the phylogenetic relations of the Neogene hypsodont horses but noted that these proposed relations were very provisional. In order to test these provisional hypothesized relations, cladistic analyses were performed on the character state matrix presented in Appendix B, which combines the taxa that Hulbert (1989) and Hulbert and MacFadden (1991) used in their separate analyses. Although the overall cladogram typologies and resulting hypothesized relationships presented herein can be compared with those presented by Hulbert (1989) and Hulbert and MacFadden (1991), a direct comparison of the cladogram lengths (number of

steps) cannot be made because each analysis was performed using a different number of taxa, characters, and character states.

Analysis of Appendix B with equally weighted characters produced two equally most parsimonious cladograms of 246 steps with consistency indices of 39 and retention indices of 66 (Figure 4). The cladograms differ only in the positions of *Acritohippus tertius* and "*Merychippus*" sp. near "*M.*" *sejunctus;* in one they are allied with the protohippines and hipparionines (Figure 4A), whereas in the other they are allied with the equines (Figure 4B). One of the cladograms of the equally weighted analysis of Appendix B (Figure 4A) is identical to the hypothesized relationships proposed by Hulbert and MacFadden (1991, fig. 13) except for the positions of the protohippines; in Hulbert and MacFadden's analysis, they are allied with the equines, whereas, in this analysis, they are allied with the hipparionines.

The analysis of Appendix B was then repeated using successively weighted characters, a procedure that has been shown to avoid the excessive weighting of multistate characters relative to binary characters and a means of basing outgroupings on more dependable characters without making prior decisions on weighting (Goldman, 1988; Farris, 1988; Hulbert and MacFadden, 1991). This procedure also reduces the ambiguity of complex data sets; there may be multiple cladograms of minimal length with equally weighted characters, but successive weighting will often produce a single most parsimonious cladogram (Farris, 1988). Thus, cladograms produced using successively weighted characters have higher consistency and retention indices and are based on more reliable characters than those produced using equally weighted characters. The successively weighted analysis of Appendix B resulted in a single most parsimonious cladogram of 556 steps with a consistency index of 53 and retention index of 77 (Figure 5). The successively weighted analysis confirms most of the hypothesized relationships proposed by Hulbert and MacFadden (1991, fig. 13) except for the following: 1) the protohippines are allied with the hipparionines instead of the equines; 2) *Acritohippus tertius* is allied with the equines instead of the hipparionines; and 3) the positions of the *Hipparion* clade and the *Neohipparion* clade ("*Merychippus*" *coloradense* [Osborn, 1918], *Pseudhipparion, Neohipparion*) are interchanged.

In order to determine the phylogenetic relations of *Acritohippus* and *Heteropliohippus* to other Neogene hypsodont horses, cladistic analyses were performed using the character state matrix presented in Appendix C, which includes 24 of the horse taxa analyzed by Hulbert (1989) and Hulbert and MacFadden (1991) plus *Acritohippus quinni, Heteropliohippus hulberti,* and "*Dinohippus*" *interpolatus.* Following Hulbert and MacFadden (1991), "*Parahippus*" *leonensis* was selected as the outgroup. *Equus simplicidens* was selected as the representative for *Equus* because it is the oldest known and least derived species of the genus (Winans, 1989; Kelly, 1994; Downs and Miller, 1994). Hulbert and MacFadden (1991) included *Protohippus vetus* J.H. Quinn, 1955, in their cladistic analysis because it is the oldest known species of *Protohippus.* However, many of the character states of *Protohippus vetus* are unknown. In the cladistic analyses presented herein, the character states for *Protohippus* were based not only on *Protohippus vetus* but also on the better known *Protohippus perditus.*

Analysis of Appendix C with equally weighted characters resulted in two equally most parsimonious cladograms of 260 steps with consistency indices of 36 and retention indices of 65 (Figure 6). These cladograms differ only in the positions of the acritohippines and "*Merychippus*" sp. near "M." *sejunctus;* in one they are allied with the equines (Figure 6A), whereas in the other they are allied with the protohippines and the hipparionines (Figure 6B). The equally weighted analysis of Appendix C supports the following conclusions: 1) *Parapliohippus carrizoensis* is a generically distinct clade that is the sister taxon of the higher equines (*Pliohippus, Heteropliohippus, Astrohippus, Dinohippus,* and *Equus*); 2) *Heteropliohippus* is the closest sister taxon to *Astrohippus* and the pliohippine clade (*Heteropliohippus, Astrohippus,* and *Pliohippus*) is monophyletic and the closest sister group to the *Equus–Dinohippus* clade; 3) the acritohippine clade (*Acritohippus tertius, Acritohippus isonesus,* and *Acritohippus quinni*) is monophyletic and its relationships to the equines or the hipparionines are unresolved; 4) the relationships of the "*Merychippus*" sp. near "*M.*" *sejunctus* clade to the acritohippines, protohippines, equines, or hipparionines are unresolved; and 5) the protohippine clade is monophyletic and the closest sister group to the hipparionines.

The analysis of Appendix C was then repeated using successively weighted characters, which resulted in a single most parsimonious cladogram of 556 steps with a consistency index of 53 and a retention index of 77 (Figure 7). The cladogram produced by the successively weighted analysis (Figure 7) is identical to one of the cladograms produced by the equally weighted analysis (Figure 6A) except for the position of "*Merychippus*" sp. near "*M.*" *sejunctus.* In the successively weighted analysis, "*Merychippus*" sp. near "*M.*" *sejunctus* represents a distinct clade that is more closely allied to the hipparionines than to the acritohippines or the equines. The successively weighted analysis of Appendix C supports the following conclusions: 1) *Parapliohippus carrizoensis* is a generically distinct clade that is the sister taxon of the higher equines (*Pliohippus, Heteropliohippus, Astrohippus, Dinohippus,* and *Equus*); 2) *Heteropliohippus* is the closest sister taxon to *Astrohippus* and the pliohippine clade (*Heteropliohippus, Astrohippus,* and *Pliohippus*) is monophyletic and the closest sister

Figure 4. Two equally most parsimonious cladograms of 246 steps with consistency indices of 39 and retention indices of 66 using the character state matrix presented in Appendix B with characters equally weighted.

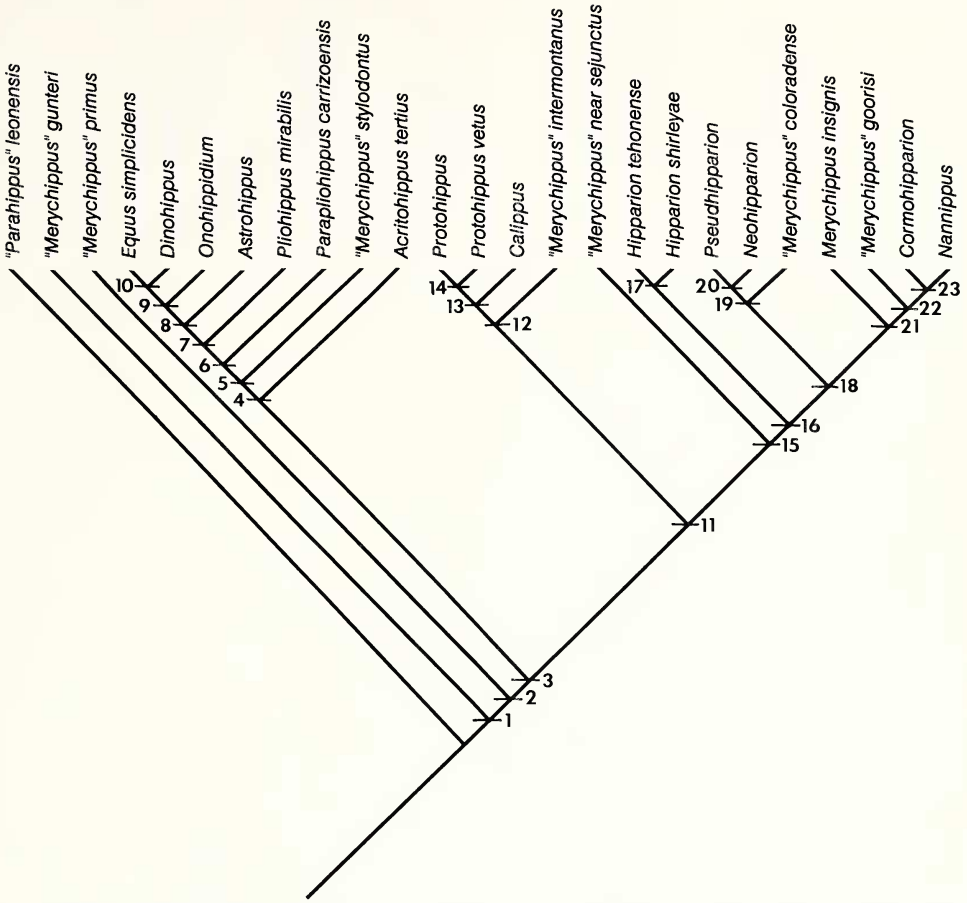

Figure 5. Single most parsimonious cladogram of 560 steps with a consistency index of 54 and retention index of 77 using the character state matrix presented in Appendix B with characters successively weighted. The cladogram is supported by the following list of ancestral synapomorphies. Number to left of period denotes character number and to right of period character state of hypothesized ancestor. Node 1: 20.1; 21.1; 30.2; 31.1; 57.1; 62.1; 70.0; 71.1. Node 2: 23.1; 27.2; 28.2; 29.1; 33.2; 38.2; 39.2; 45.1; 55.1; 56.1. Node 3: 2.1; 5.1; 21.2; 45.2; 54.1; 70.2; 71.2. Node 4: 12.1; 30.1; 33.1; 67.1. Node 5: 3.2; 27.0; 28.0. Node 6: 20.2; 63.1; 70.3; 71.6. Node 7: 5.2; 23.2; 29.1; 43.1; 62.2; 63.2; 71.7. Node 8: 1.2; 3.2; 7.1; 12.0; 38.2; 39.2; 70.4. Node 9: 5.0; 30.1; 33.2; 38.0; 39.0. Node 10: 79.1. Node 11: 52.1; 71.3. Node 12: 7.1; 12.0; 23.2; 31.1; 43.1; 66.1; 67.1. Node 13: 16.0; 28.1; 48.2; 63.1. Node 14: 13.1; 40.0; 41.0. Node 15: 31.2; 33.3; 55.2. Node 16: 7.1; 12.0; 27.4; 28.4; 39.1. Node 17: 1.1; 6.1; 7.2; 23.2; 33.4; 35.0; 38.1; 48.1. Node 18: 35.2; 48.2. Node 19: 23.2; 33.3; 43.1; 62.2; 63.1; 71.4. Node 20: 3.0; 5.0; 16.1; 20.2; 22.1; 23.3; 31.1; 52.2; 63.2; 71.7. Node 21: 5.2; 30.3; 32.1; 33.4; 38.1; 39.1. Node 22: 3.2; 5.3; 6.1; 27.5; 28.5; 33.5; 38.0; 39.0; 40.0; 52.2. Node 23: 3.3; 7.2; 20.2; 23.2; 29.0; 43.1; 62.2; 63.1; 71.5.

group of the *Equus–Dinohippus* clade; 3) the acritohippine clade (*Acritohippus tertius, Acritohippus isonesus,* and *Acritohippus quinni*) is monophyletic and the closest sister group to the equines; and 4) the protohippine clade is monophyletic and the closest sister group of the hipparionines.

In the successively weighted analysis of Appendix C (Figure 7), a single hypothesized ancestral synapomorphy unites the acritohippines with the equines (Figure 7, node 4); a malar fossa is present that is well separated from the DPOF (character 12.1). In this analysis, the acritohippines are assumed to be derived relative to the equines by the character transformation of an ancestral well-separated DPOF and malar fossa to a confluent DPOF and malar fossa. This scenario cannot be supported or refuted by the geochronological distribution of these clades because the earliest known acritohippine, *Acritohippus tertius,* and the earliest known equine, *Parapliohippus carrizoensis,* first appeared at about the same time in the late Hemingfordian. Considering the variability of the position of the acritohippines within the cladograms presented herein and those of Hulbert (1989) and Hulbert and MacFadden (1991), I regard the relationships of the acritohippines to the equines and hipparionines as uncertain.

Hulbert and MacFadden (1991) listed the fol-

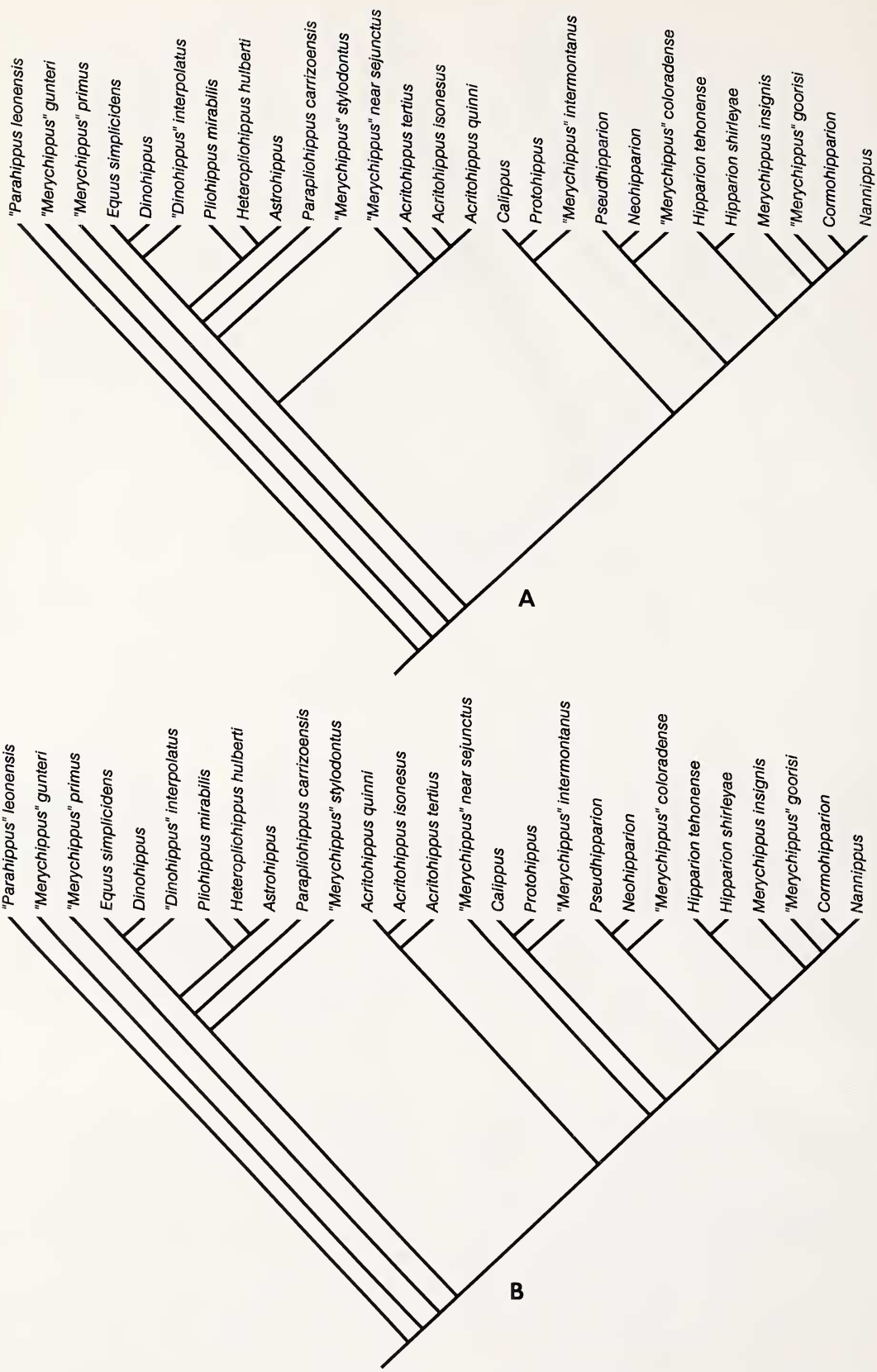

Figure 6. Two equally most parsimonious cladograms of 260 steps with consistency indices of 36 and retention indices of 65 using the character state matrix presented in Appendix C with characters equally weighted.

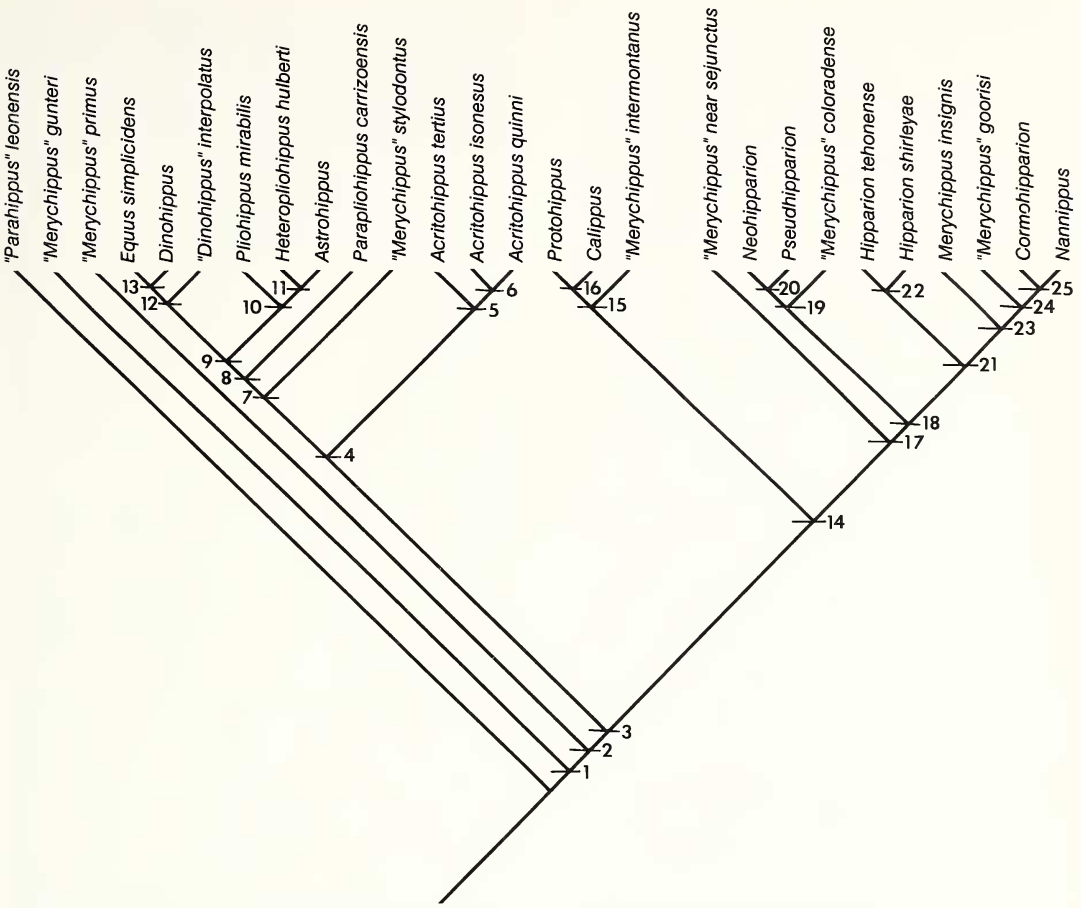

Figure 7. Single most parsimonious cladogram of 556 steps with a consistency index of 53 and retention index of 77 using the character state matrix presented in Appendix C with characters successively weighted. The cladogram is supported by the following list of ancestral synapomorphies. Number to left of period denotes character number and to right of period character state of hypothesized ancestor. Node 1: 20.1; 21.1; 30.2; 31.1; 57.1; 62.1; 70.0; 71.1. Node 2: 23.1; 27.2; 28.2; 29.1; 33.2; 38.2; 39.2; 45.1; 55.1; 56.1. Node 3: 2.1; 3.1; 21.2; 45.2; 54.1; 70.2; 71.2. Node 4: 12.1. Node 5: 12.2; 16.1; 27.3; 31.2. Node 6: 3.2; 5.2; 28.3. Node 7: 30.1; 33.1; 67.1. Node 8: 5.2; 16.2; 27.0; 28.0. Node 9: 20.2; 63.1; 70.3; 71.6. Node 10: 3.2; 38.3; 39.3. Node 11: 7.0; 43.1; 67.0. Node 12: 1.2; 3.1; 7.2; 33.2; 38.1; 39.1; 62.2; 63.2; 70.4; 71.6; 72.1. Node 13: 5.0; 12.0; 23.2; 38.0; 39.0; 71.7. Node 14: 48.2; 52.1; 71.3. Node 15: 7.1; 23.2; 43.1; 66.1; 67.1. Node 16: 16.0; 28.1; 63.1. Node 17: 31.2; 33.3; 55.2. Node 18: 27.4; 28.4; 39.1. Node 19: 23.2; 35.2; 43.1; 62.2; 63.1; 71.4. Node 20: 3.0; 5.0; 7.1; 16.1; 20.2; 22.1; 23.3; 31.1; 52.2; 63.2; 71.7. Node 21: 7.1; 33.4; 38.1. Node 22: 1.1; 6.1; 7.2; 23.2; 35.0; 48.1. Node 23: 5.2; 30.3; 32.1; 35.2. Node 24: 3.2; 5.3; 6.1; 27.5; 28.5; 33.5; 38.0; 39.0; 40.0; 52.2. Node 25: 3.3; 7.2; 20.2; 23.2; 29.0; 43.1; 62.2; 63.1; 71.5.

lowing six hypothesized ancestral synapomorphies that unite the protohippines and the equines in the tribe Equini: 1) the DPOF depth is moderate; 2) the DPOF has a shallow posterior pocket; 3) the P3–4 protocones connect to the protolophs in early wear; 4) hypoconal lakes are formed on P3–4 with closure of the hypoconal grooves; 5) the p3–4 metastylids are notably smaller and positioned more lingually than the metaconids; and 6) the m1–3 metastylids are notably smaller and positioned more labially than the metaconids. The first four synapomorphies listed above are not actually shared by all protohippines. The DPOF is moderately deep in "*Merychippus*" *intermontanus* (Merriam, 1915), shallow in *Protohippus*, and very shallow in *Calippus*. The connection of the P3–4 protocones to the protolophs occurs in early wear for "*M.*" *intermontanus* and *Protohippus*, but in *Calippus* it occurs at the onset of wear, which may represent a reversal or a further derived state. The formation of hypoconal lakes on the P3–4 occurs in "*M.*" *intermontanus* and *Calippus*, but not in *Protohippus*. If the six hypothesized synapomorphies actually occurred in the proposed ancestor of the protohippines and equines, then at least three character state reversals must have occurred in the protohippines. Of these six synapomorphies, only the following can be observed in all of the protohippines: 1) the p3–4 metastylids are notably smaller and positioned more lingually than the metaconids; and 2) the m1–

2 metastylids are notably smaller and positioned more labially than the metaconids. Furthermore, certain hipparionines exhibit the same derived character states as numbers 1, 2, and 4 of the above six hypothesized synapomorphies (Hulbert, 1987a, 1988b). If the protohippines shared a common ancestor with the equines, then it must be assumed that certain hipparionines independently derived these character states and, therefore, these character states are prone to convergence or parallelism. Moreover, in *Parapliohippus carrizoensis* and "*Merychippus*" *stylodontus,* the least derived and oldest unequivocal equines, the p3–4 metastylids and metaconids are subequal or equal in size and position. This fact necessitates the assumption that, in *P. carrizoensis* and "*M.*" *stylodontus,* the p3–4 metastylids underwent a character state reversal from the synapomorphous character state of the hypothesized ancestor of the protohippines and equines. Another possible scenario is that later equines, such as *Pliohippus,* and the protohippines independently acquired this character state transformation. As Szalay (1993) and K.M. Scott and Janis (1993) have demonstrated, cladistic analyses based on algorithms using parsimony will only produce a phylogenetic hypothesis with the least number of steps, which often necessitates the inclusion of biologically unlikely character transformations. K.M. Scott and Janis (1993) also noted that characters utilized as synapomorphies should be well corroborated and not prone to functional or ecological homoplasy. Furthermore, in exclusive cladistic practice, the geochronologic distributions of taxa are disregarded in determining a phylogenetic hypothesis, which can also result in biologically improbable character transformations (Szalay, 1993). Thus, the only synapomorphy listed by Hulbert and MacFadden (1991) that can be used with confidence to unite the protohippines with the equines is that the m1–2 metastylids are notably smaller and positioned more labially than the metaconids. However, as previously noted, the morphology of the lower molar metaconid–metastylid complex may be prone to homoplasy as a functional adaptive response to feeding strategy.

In all the analyses presented herein, the protohippines are united with the hipparionines by the following hypothesized ancestral synapomorphies: 1) the dp3–4 protostylids are well developed; 2) the p3–m3 protostylids are well developed; and 3) the unworn molar crown height is about 35 mm. The ancestral synapomorphy of well-developed dp3–4 protostylids is shared by most all hipparionines. However, in certain equines, such as *Astrohippus* and *Dinohippus,* moderately well-developed dp3–4 protostylids were secondarily derived (Hulbert, 1987a, tab. 46), indicating that this character may be prone to convergence. The ancestral synapomorphy of having moderately well-developed p3–m3 protostylids is transformed to the more derived state of very well-developed protostylids in certain hipparionines, such as in *Nannippus, Pseudhipparion, Neohipparion,* and *Cormohipparion.* Excluding the protohippines, almost all equines, such as *Pliohippus, Dinohippus, Astrohippus, Onohippidium,* and most species of *Equus,* exhibit the derived state of the loss of the p3–m3 protostylids (Hulbert, 1987a, tab. 46). However, in very rare instances certain equines, such as *Heteropliohippus hulberti* and *Equus parastylidens* Mooser, 1959, have secondarily acquired the derived character state of moderately developed p3–m3 protostylids, indicating that this character may be prone to a very low degree of convergence. The ancestral synapomorphy of an unworn crown height of 35 mm is transformed to a more derived state of greater hypsodonty in all hipparionines. The trend toward greater hypsodonty in more derived taxa is also observed in the equines and acritohippines and appears to be a functional adaptive transformation. Considering the above facts, the only ancestral synapomorphy that can be used with any confidence to unite the protohippines with the hipparionines is moderately to well-developed p3–m3 protostylids. However, it should be noted that the protohippines do exhibit similarities in facial morphology with certain hipparionines. For example, the oldest protohippines for which the facial morphology is known, the early to late Barstovian "*Merychippus*" *intermontanus* and the late Barstovian *Protohippus perditus,* exhibit the following similarities in facial morphology with specimens of the hipparionine "*Merychippus*" *coloradense* from the early Barstovian of Nebraska: 1) the DPOF is elongate oval-shaped, slightly pocketed posteriorly, moderately well rimmed posteriorly, and positioned relatively high and anterior on the face, resulting in a moderately wide preorbital bar; and 2) a malar fossa is lacking.

Because the character transformations in the cheek teeth of Neogene hypsodont horses exhibit high degrees of convergence, reversal, and parallelism (Hulbert, 1987a, 1989; Hulbert and MacFadden, 1991; this paper), neither the proposed phylogenetic hypothesis of Hulbert and MacFadden (1991), which unites the protohippines with the equines, nor those presented herein, which unite the protohippines with the hipparionines, appear overly convincing. Based on the cladistic analyses presented herein, I regard the protohippines as the sister group of the hipparionines, but realizing that this proposed relationship is very tentative. The hypothesis that the protohippines are more closely allied with the hipparionines than the equines (Figures 4–7) is very similar to an alternative, slightly less parsimonious cladogram presented by Hulbert and MacFadden (1991, fig. 11B), which places the equines as the sister group of the hipparionines and protohippines.

In the successively weighted cladistic analyses presented herein, "*Merychippus*" sp. near "*M.*" *sejunctus* is the least derived hipparionine and is the closest sister taxon to all other hipparionines. This is based on the assumption that "*M.*" sp. near "*M.*"

sejunctus possesses the following ancestral synapomorphies with other hipparionines: 1) well-developed M1–3 plis caballin (character 31.2); 2) persistent P2–M3 internal fossette plications (character 33.3); and 3) persistently well-separated metaconids and metastylids (character 55.2). "*Merychippus*" *sejunctus*, the presumed anagenetic descendant of "*M.*" sp. near "*M.*" *sejunctus* (Hulbert and MacFadden, 1991), is plesiomorphic for the above character states. This fact is problematical because it would require three character state reversals for "*M.*" *sejunctus* to be derived from "*M.*" sp. near "*M.*" *sejunctus*. These character transformations seem unlikely but are possible considering the high degree of homoplasy exhibited in the cheek teeth character states of Neogene hypsodont horses. "*Merychippus*" sp. near "*M.*" *sejunctus* and the acritohippines have a similar facial morphology, wherein the DPOF and malar fossa are confluent. The successively weighted cladistic analyses assume that this apomorphic facial morphology was independently derived in "*M.*" sp. near "*M.*" *sejunctus* and the acritohippines. This assumption seems biologically unlikely because, in many other Neogene hypsodont horses, a similar facial morphology is generally a good indicator of a close phylogenetic relationship (MacFadden, 1984a). However, the oldest known acritohippine, *Acritohippus tertius*, which first appeared in the late Hemingfordian, is plesiomorphic for the three derived cheek teeth character states exhibited by the early Barstovain "*M.*" sp. near "*M.*" *sejunctus*. An alternative scenario to explain a similar facial morphology in "*M.*" sp. near "*M.*" *sejunctus* and the acritohippines is that "*M.*" sp. near "*M.*" *sejunctus* was derived from *A. tertius* or a similar ancestral morphotype with a confluent DPOF and malar fossa and, with this speciation event, it independently developed stronger molar plis caballin, more persistent P2–M3 internal fossettes, and better separated metaconids and metastylids as a functional dietary response. In this scenario, *Acritohippus* would become the closest sister taxon to "*M.*" sp. near "*M.*" *sejunctus* and the three character state transformations observed in "*M.*" sp. near "*M.*" *sejunctus* would represent convergence with the hipparionines, not synapomorphies. Considering the high degree of homoplasy observed in the cheek teeth morphology of Neogene hypsodont horses and the similarity in facial morphology of "*M.*" sp. near "*M.*" *sejunctus* and *Acritohippus*, I regard the position of "*M.*" sp. near "*M.*" *sejunctus* in the successively weighted cladograms (Figures 5, 7) as equivocal and its phylogenetic status as unresolved. If "*M.*" sp. near "*M.*" *sejunctus* is removed from the analyses, then the Hipparionini *s.s.* would include *Neohipparion, Pseudhipparion, Hipparion, Nannippus, Cormohipparion, Merychippus s.s.*, and "*Merychippus*" *coloradense*.

In summary, the analyses presented herein support many of the results of the cladistic analyses of Hulbert (1989) and Hulbert and MacFadden (1991), with the exception of the following: 1) the pliohippines (*Heteropliohippus, Astrohippus*, and *Pliohippus*) form a monophyletic clade that is the closest sister group of the *Onohippidium–Hippidion* clade and *Equus–Dinohippus* clade; 2) the acritohippines (*Acritohippus tertius, A. isonesus*, and *A. quinni*) form a monophyletic clade whose relations to the equines and hipparionines remain unresolved; and 3) the protohippines ("*Merychippus*" *intermontanus, Protohippus*, and *Calippus*) form a monophyletic clade that is the closest sister group of the hipparionines.

Hulbert (1989) and Hulbert and MacFadden (1991) argued for a basal dichotomy in the late Neogene hypsodont horses that equated with the tribal ranks of the Equini and Hipparionini, which in the successively weighted analyses presented herein would be equated with nodes 4 and 11 of Figure 5 and nodes 4 and 14 of Figure 7, respectively. According to this contention, the acritohippines and protohippines represent monophyletic clades of subtribal rank. However, as demonstrated in the analyses presented herein and those of Hulbert (1989) and Hulbert and MacFadden (1991), the position of the acritohippines in the cladograms is highly labile, making any hypothesis of their relationships to the equines or hipparionines equivocal. Furthermore, two of the three putative ancestral synapomorphies defining the nodes that unite the protohippines with the hipparionines (e.g. node 11, Figure 5; node 14, Figure 7) are equivocal. Basing a tribal rank on a small number of putative ancestral synapomorphies may not be prudent because it is well documented that many of the morphological character states of the late Neogene hypsodont horses are homoplasous; that is, they exhibit a high degree of parallelism, convergence, and reversal in response to the functional requirements of feeding and locomotion (Hulbert, 1987a, 1989; MacFadden, 1992; this paper). According to this contention, the four clades (acritohippines, protohippines, equines, and hipparionines) could be equated with tribal ranks and the nodes of the basal dichotomy regarded as unnamed ranks.

The following is a conservative assessment of the phylogenetic relationships of the late Neogene hypsodont horses based on a consensus of all the analyses presented herein. "*Merychippus*" *gunteri* (Simpson, 1930) and "*Merychippus*" *primus* are the inferred successive sister taxa to all other Neogene hypsodont horses. Following the cladogenetic speciation events that produced "*M.*" *gunteri* and "*M.*" *primus*, four additional basal monophyletic clades of Neogene hypsodont horses evolved; the Equini *s.s.*, the Hipparionini *s.s.*, the Protohippini *s.s.*, and the acritohippines. The Protohippini *s.s.* are provisionally regarded as the closest sister group to the Hipparionini *s.s.* The relationships of the acritohippines to the Equini *s.s.* and the Hipparionini *s.s.* are unresolved. The relationships of "*Merychippus*" sp. near "*M.*" *sejunctus* to the Hipparionini *s.s.* and the acritohippines remains unclear. The

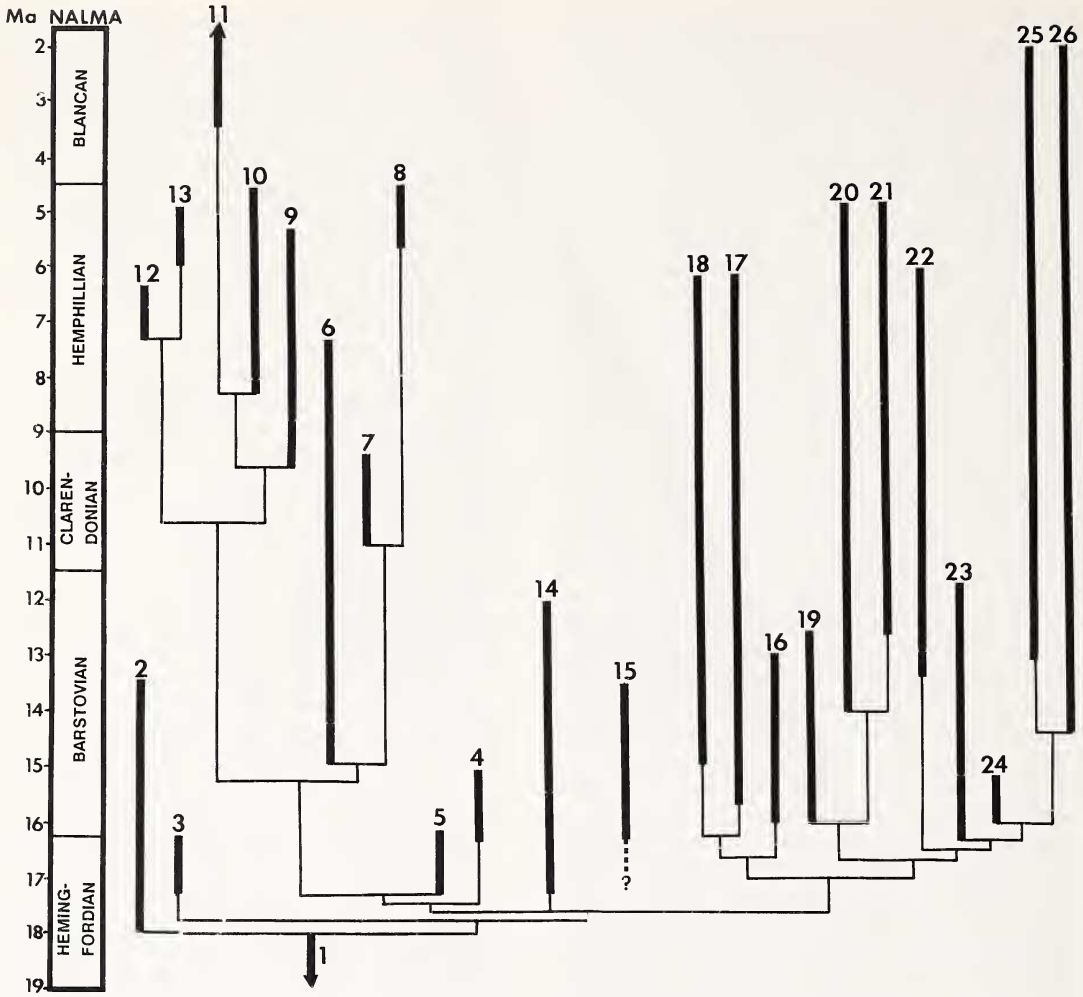

Figure 8. Hypothesized phylogenetic tree of late Neogene hypsodont horses. Thick vertical line indicates geochronologic occurrence of taxon. Key to taxa: 1, "*Parahippus*" *leonensis;* 2, "*Merychippus*" *gunteri;* 3, "*Merychippus*" *primus;* 4, "*Merychippus*" *stylodontus;* 5, *Parapliohippus carrizoensis;* 6, *Pliohippus;* 7, *Heteropliohippus;* 8, *Astrohippus;* 9, "*Dinohippus*" *interpolatus;* 10, *Dinohippus;* 11, *Equus;* 12, *Onohippidium;* 13, *Hippidion;* 14, *Acritohippus;* 15, "*Merychippus*" sp. near "*M.*" *sejunctus*/"*M.*" *sejunctus* clade; 16, "*Merychippus*" *intermontanus;* 17, *Protohippus;* 18, *Calippus;* 19, "*Merychippus*" *coloradense;* 20, *Neohipparion;* 21, *Pseudhipparion;* 22, *Hipparion;* 23, *Merychippus;* 24, "*Merychippus*" *goorisi;* 25, *Nannippus;* 26, *Cormohipparion.*

Equini *s.s.* are united by the following ancestral synapomorphies: 1) the DPOF depth is moderate; 2) the malar fossa is distinct, always present, and well separated from the DPOF; 3) the P2–4 plis caballin are commonly present, but small and nonpersistent (disappear in early to moderate wear); 4) the plications of the internal fossette margins are very simple and nonpersistent; and 5) the m1–3 metastylids are notably smaller in size and positioned more labially than the metaconids. The Hipparionini *s.s.* are united by the following ancestral synapomorphies: 1) the M1–3 plis caballin are well developed; 2) the P3–M2 protocones connect with the protolophs in late moderate wear; 3) the internal fossette margins are simple, but persistent (present in moderate to late wear); 4) the M1–2 hypoconal grooves close in late wear; 5) the p3–m3 metaconids and metastylids are persistently well separated; and 6) metacarpal V articulates primarily with metacarpal IV. The Protohippini *s.s.* are united by the following ancestral synapomorphies: 1) the relative PBL is moderate; 2) the P3–M2 protocones have elongated oval occlusal outlines; 3) the M1–3 plis caballin are commonly present, but small and nonpersistent; 4) the upper cheek teeth are moderately curved; 5) the p3–4 metastylids are smaller and positioned more lingually than the metaconids; and 6) the m1–3 metastylids are notably smaller and positioned more labially than the metaconids. The acritohippines are united by the following ancestral synapomorphies: 1) the malar fossa is shallow, always present, and confluent with the DPOF;

2) the relative muzzle length is moderate; 3) the upper cheek teeth are moderately curved; 4) the P3–4 protocones connect with the protolophs in early moderate wear; and 5) the M1–3 plis caballin are moderately well developed and relatively persistent. Based on this assessment, a hypothesized phylogenetic tree was constructed and is presented in Figure 8.

In conclusion, all the analyses presented herein indicate that after the cladogenetic speciation events that produced "*Merychippus*" *gunteri* and "*Merychippus*" *primus* the Neogene hypsodont horses underwent rapid cladogenesis, resulting in at least four additional basal monophyletic lineages: the Equini *s.s.*, the Hipparionini *s.s.*, the Protohippini *s.s.*, and the acritohippines. However, any phylogenetic hierarchical classification depicting the interrelationships of these four additional lineages is very tentative and will probably require modification with further study or the discovery of additional diagnostic characters.

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APPENDICES

Appendix A

Characters and character states used in cladistic analyses presented herein.

Except as noted in text, numbering scheme and descriptions of characters and character states correspond to those of Hulbert (1988b, 1989) and Hulbert and MacFadden (1991).

1. Depth of nasal notch. Four states are recognized: 0, posteriormost point dorsal to about the anterior three quarters of C–P2 diastema or more anterior; 1, posteriormost point dorsal to anterior half of P2 or just anterior to P2; 2, posteriormost point dorsal to posterior half of P2–3; 3, posteriormost point dorsal to P4 or deeper.
2. Frontal bones. Two states are recognized: 0, frontal bones notably domed; 1, frontal bones flat, not domed.
3. Depth of DPOF. The DPOF is a depression of varying depth and morphology present in many fossil equids. Four states are recognized: 0, depth of fossa relative to the surrounding surface of the skull very shallow, maximum depth less than 5 mm; 1, depth shallow, about 5–10 mm; 2, depth moderate, 10–15 mm; 3, depth deep, greater than 15 mm.
4. Anterior margin DPOF (character 4, Hulbert, 1988b; character 7, Hulbert, 1989). Two states are recognized: 0, anterior margin of DPOF confluent with face without a rim; 1, anterior margin well defined with a pronounced rim.
5. Posterior margin and pocket of DPOF. Four states are recognized: 0, posterior margin of DPOF without a pronounced rim, no pocket; 1, posterior margin with a pronounced rim, but not pocketed; 2, posterior margin with rim and shallow pocket, less than 5 mm deep; 3, posterior margin with rim and pocket depth greater than 5 mm. A pronounced rim means that the margin of the fossa is very easily discernible because of a distinct change in slope.
6. Distinct ventral rim on DPOF. Two states are recognized: 0, ventral rim of DPOF without distinct or pronounced margin; 1, ventral rim distinctly rimmed.
7. Relative PBL. The PBL is the distance between the orbit and the DPOF. Relative PBL is determined by dividing it by UTRL. Three states are recognized: 0, narrow (ratio < 0.10); 1, moderate (ratio 0.10–0.20); 2, long (ration > 0.20).
11. Zygomatic buckle (Hulbert, 1989; also see Webb, 1969). Two states are recognized: 0, present; 1, absent.
12. Malar fossa (character 10, Hulbert, 1989; character 12, Hulbert and MacFadden, 1991). In addition to a DPOF, some equids have a depression in the ventral preorbital region termed a malar fossa. Three states are recognized: 0, absent or occasionally present as a very slight depression; 1, distinct malar fossa always present and well separated from DPOF; 2, distinct malar fossa always present and confluent with DPOF.
13. Muzzle width relative to UTRL at moderate wear stage. Two states are recognized; 0, moderate or narrow; 1, broad ($> 36\%$).
14. Incisor arcade. Two states are recognized: 0, arcuate; 1, straight.
16. Relative muzzle length. Character state is determined by comparison of upper I3–P2 diastema length (UDL) and UTRL in middle-age adults. Four states are recognized: 0, short (UDL $< 40\%$ UTRL); 1, moderate (UDL between 40 and 55% of UTRL); 2, elongated (UDL between 56 and 70% UTRL); 3, very elongated (UDL $> 70\%$ of UTRL).
20. Cement on deciduous premolars. Three states are recognized: 0, no cement present; 1, cement layer rudimentary and very thin (< 1 mm thick), commonly only found on dP4 and dp4; 2, moderate to very thick coating (> 1 mm thick) of cement on all deciduous cheek teeth.
21. Cement on permanent cheek teeth. Three states are recognized: 0, thin layer of cement present, < 1 mm in thickness; 1, moderate layer of cement present, about 1 mm thick; 2, thick (> 1.5 mm) layer of cement present, as in *Equus.*
22. Orientation of long axis of the protocone of P2–4. Two states are recognized: 0, approximately anteroposteriorly; 1, markedly anterolabial-posterolingually.
23. Protocone shape (P3–M2). Based on average value of ratio of PRL to PRW, taken in moderate wear stages. Four states are recognized: 0, round (ratio < 1.2); 1, oval (ratio 1.2–2.0); 2, elongate oval (ratio 2.1–3.0); 3, elongate (ratio > 3.0).
26. P2 anterostyle. Two states are recognized: 0, large, expanded; 1, reduced.
27. Timing of protocone connection to protoloph on the P3 and P4. Seven states are recognized: 0, protocone connected to protoloph immediately after onset of occlusal wear; 1, connected during the very early wear stage; 2, connected during the early wear stage; 3, connected during the early moderate wear stage; 4, connected during the late moderate wear stage; 5, connected during the late wear stage; 6, protocone isolated from protoloph to base of crown.
28. Timing of protocone connection to protoloph on the M1 and M2. Same seven states as character 27.
29. Protocone connection to hypocone on M1 and M2. Three states are recognized: 0, protocone never connects to hypocone; 1, connection occurs only in late wear stage; 2, connection occurs prior to late wear stage.
30. Pli caballin on P2–4. Four states are recognized: 0, pli caballin absent or very rare; 1, pli caballin common, but small (< 2 mm) and nonpersistent; 2, pli caballin well developed, relatively persistent, commonly single or unbranched; 3, pli caballin well de-

veloped, persistent, commonly branched or multiple.

31. Pli caballin on M1–3. Same four states as character 30.
32. External fossette plications. Three states are recognized: 0, pli protoloph and pli hypostyle rare or, if present, single and nonpersistent; 1, pli protoloph and/or pli hypostyle common, persistent, but single; 2, multiple pli protoloph and/or pli hypostyle present in early wear stages.
33. Internal fossette plications. This character is based on the common fossette morphology observed in early and moderate wear stages. Six states are recognized: 0, all internal fossette plications (pli prefossette, pli postfossette, etc.) absent, or very rare (if present simple, shallow, and nonpersistent); 1, very simple internal fossette plications (pli prefossette and pli postfossette single or absent, can be deep, prefossette loop not prominent); 2, simple but nonpersistent internal fossette plications (pli prefossette and pli postfossette multiple in early wear stages, single in moderate wear stages, absent in late wear stages) that are shallow and nonbranching; 3, simple but persistent internal fossette plications (as in 2 but with plications generally present in later wear stages); 4, moderately complex internal fossette plications (two to five plications present on each side in early and moderate wear stages, with a limited amount of branching); 5, complex internal fossette plications (three to seven plications present on each side in early and moderate wear stages, branching of plications common).
35. Metastyle development. Three states are recognized: 0, metastyle generally absent or very weak; 1, metastyle common but not strong; 2, metastyle very well developed.
38. Timing of hypoconal groove closure on P2–4. Four states are recognized: 0, hypoconal groove open to near the base of the crown; 1, hypoconal groove closed in late wear stages; 2, hypoconal groove closed in moderate wear stages; 3, hypoconal groove closed in early wear stages.
39. Timing of hypoconal groove closure on M1–2. Same four states as character 38.
40. Hypoconal lake on P3–4. Two states are recognized: 0, hypoconal groove does not form an isolated lake when it closes; 1, hypoconal groove does form a lake after closing.
41. Hypoconal lake on M1–2. Same two states as character 40.
43. Curvature of upper cheek teeth (P3–M2). Based on the ROC measured along the mesostyle (Skinner and Taylor, 1967). Three states are recognized: 0, strongly curved (ROC < 40 mm); 1, moderately curved (ROC from 40 to 80 mm); 2, relatively straight (ROC > 80 mm).
45. Retention of the dp1. Three states are recognized: 0, dp1 relatively large, commonly retained with permanent dentition; 1, dp1 very reduced (diameter < 2 mm), variable present with adult dentition; 2, dp1 very rarely present with permanent dentition; vestigial if present.
48. Strength of protostylids on dp3–4. Three states are recognized: 0, protostylids weak, may be present only near base of crown as small anterior cingulids, and do not appear on the occlusal surface until late wear stages; 1, protostylids moderately well developed, positioned in anterolabial corner of the tooth, appear in early wear stage; 2, protostylids very well developed, extend labially about as far as the protoconid, straight.
52. Strength of protostylids on p3–m3. Same three states as character 48.
54. Expansion of metaconid–metastylid complex. Three states are recognized: 0, metaconid–metastylid relatively small and unexpanded (MML of p3 or p4 averages < 45% of APL); 1, metaconid–metastylid expanded but not elongated (MML of p3 or p4 averages between 45 and 50% of APL); 2, metaconid–metastylid moderately elongated (MML of p3 or p4 > 50% of APL).
55. Separation of metaconid and metastylid on p3–m3. Three states are recognized: 0, metaconid and metastylid not well separated from one another even in very early wear stages; 1, well separated from each other only in very early and early wear stages; 2, persistently well separated from each other. Well separated means that the areas of exposed dentine of the metaconid and metastylid are distinctly separated from each other by the linguaflexid, ectoflexid, metaflexid, and entoflexid, with only a narrow passage of dentine connecting them.
56. Metaconid–metastylid on p2. Two states are recognized: 0, single median lingual cuspid present, not separated into metaconid and metastylid; 1, separate metaconid and metastylid present on p2, at least in early wear stage.
57. Development of pli entoflexid. Two states are recognized: 0, pli entoflexid absent or rudimentary; 1, pli entoflexid commonly present, at least in early and very early wear stages.
62. Ectoflexid depth on p2. Three states are recognized: 0, ectoflexid deep, completely penetrates isthmus; 1, ectoflexid moderately deep, only partially penetrates isthmus; 2, ectoflexid shallow, does not penetrate isthmus.
63. Ectoflexid depth on p3–4. Same three states as character 62.
66. Relative size of metaconid and metastylid on p3–4. Two states are recognized: 0, metaconid and metastylid equal or subequal in size; 1, metastylid notably smaller than metaconid and located more lingually.
67. Relative size of the metaconid and metastylid on m1–m3. Two states are recognized: 0, metaconid and metastylid equal or subequal in size and position of their lingual borders; 1, metastylid notably smaller than metaconid, lingual border located more labially than that of metaconid especially in moderate and late wear stages.
70. Tooth row length (character 43, Hulbert, 1989; character 70, Hulbert and MacFadden, 1991). This character is used as an indicator of overall size and reflects the mean UTRL in moderate wear stage. Five states are recognized: 0, less than 90 mm; 1, about 90–105 mm; 2, about 105–125 mm; 3, about 126–140 mm; 4, greater than 140 mm.
71. Unworn molar crown height. This character is determined by unworn M1 mesostyle crown height or m1 metaconid crown height, ±2.5 mm. Eight states are recognized: 0, less than 22 mm; 1, about 25 mm; 2, about 30 mm; 3, about 35 mm; 4, about 40 mm; 5, about 45 mm; 6, about 50 mm; 7, > 50 mm.
72. Number of digits (character 44, Hulbert, 1989). Two states are recognized: 0, tridactyl; 1, monodactyl.
79. Articulation of metacarpal V. Two states are recognized: 0, metacarpal V articulates primarily on the unciform, articulation facet for metacarpal IV absent or smaller than that for unciform; 1, metacarpal V articulates primarily on metacarpal IV, articulation facet for unciform absent or smaller than that for metacarpal IV.

Appendix B

Combined character state matrix for the two groups of taxa previously analyzed separately by Hulbert (1989) and Hulbert and MacFadden (1991) and using characters and character states presented in Appendix A

| | Characters | | |

Appendix C

Character state matrix for selected Neogene hypsodont horses using character and character states presented in Appendix A

| | Characters | | |